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VOLUME 19, NO. 1 MAY 1950

LOCAL AND SEASONAL VARIATIONS IN RELATIVE FREQUENCIES OF SPECIES OF *DROSOPHILA* IN BRAZIL

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(With 1 Figure in the Text)

1. INTRODUCTION

Drosophila is a genus of flies which contains some five to six hundred described species and doubtless many as yet undescribed ones. The natural food of *Drosophila* is seldom known with precision; for example, larvae of *D. pseudoobscura* Frolowa,† one of the species most used in population studies, have never been found under strictly natural conditions. It is, nevertheless, possible to state in a general way that both adult flies and larvae feed on yeasts and bacteria which occur in fermenting substances rich in carbohydrates, such as fruits, fungi, tree sap and, in the tropics, fleshy flowers. In accordance with this, the usual technique of collecting *Drosophila* consists in attracting them to bait of fermenting banana or other fruits, or in looking for them on natural bait of the kinds mentioned above.

Different species of *Drosophila* differ in food preferences. Some fungus-feeding species seldom or never come to fermenting fruit, and vice versa. It will be shown in this article that different kinds of fruit are attractive to different species. However, except for the fungus feeders, the food specialization is not rigid, and the same fruit or other food source is usually exploited by several species. For this reason, sympatric species of *Drosophila* may be regarded as a community which depends upon a common source of food substances, for which the different species compete with each other. The competition is more keen among species which have many common food preferences than between species which live on different foods and seldom come in contact with each other. The intensity of competition depends also upon the variety of ecological niches present in the environment: if numerous ecological niches are available, in some of them a species is likely to meet fewer competitors than in others, or may even become a monopolist.

The number of species of *Drosophila* is, in general, greater in the tropics, less in the temperate, and least in the cold zones; it is greater in humid and forested than in dry, steppe, or desert regions. Brazil has a rich fauna of *Drosophila*, and the variety of ecological niches open to Drosophilae in Brazilian forests is very large owing to the presence of many species of fruit-bearing trees and other food sources. *Drosophila* communities, in Brazilian forests, are ecological systems of great complexity. Such systems may have interesting properties not present in simpler systems found in temperate climates.

The present article reports the results of a survey of *Drosophila* populations in Brazil made chiefly during the school year, 1948–9. This survey is obviously an exploratory one, although we had the opportunity of making a cursory examination of *Drosophila* populations in the principal bioclimatic provinces of Brazil, including some rather remote and inaccessible regions.

2. MICROGEOGRAPHIC VARIATIONS

Dobzhansky (1939) noted that in Mexico and in Guatemala different assortments of species of *Drosophila* may often be found within 100–200 ft. of each other. Timoféeff-Ressovsky & Timoféeff-Ressovsky (1940) were, however, the first to submit this phenomenon to systematic study. They built, in the vicinity of Berlin, experimental fields consisting of *Drosophila* bait (nature not stated) arranged checkerboard fashion at 10 m. intervals (fields 70×90 and 110×110 m. were used). Recording of numbers of flies of different species that came to bait at different points disclosed that within these experimental fields the flies were not distributed at random, but formed nuclei of high concentration separated by relatively sparsely populated areas. These non-uniformities were more strongly pronounced in some species (*D. melanogaster* Meigen, *D. funebris* Fabricius) than in others (species of the *D. obscura* group). Dobzhansky & Epling (1944) and Dobzhansky & Wright (1943, 1947) observed in mountain forests of California that *D. pseudoobscura* forms nuclei of high concentration in the vicinity of old or diseased oak and pine trees. These non-uniformities are less striking than those found by Timoféeff-Ressovsky & Timoféeff-Ressovsky in *D. melanogaster* and *D. funebris*, and

* Contribution No. 5 of the co-operative research project of the University of São Paulo and Columbia University on genetics and ecology of tropical *Drosophila*.

† Species authorities are given in Tables 4 or 6 or where first mentioned (if in text only).

are comparable with those in the species of the *D. obscura* group. The different degrees of non-uniformity may, in part, reflect the greater mobility of *D. pseudoobscura* as compared to *D. melanogaster* and *D. funebris*. Dobzhansky & Epling found that, under summer conditions on Mount San Jacinto, California, *D. pseudoobscura* is attracted to fermenting banana bait from distances within a 40–60 m. radius from the location of the bait. One may infer that these distances are smaller in *D. melanogaster* and *D. funebris*.

Chiefly for the purpose of their study of dispersal rates in *D. willistoni* Sturtevant, some cross-shaped experimental fields were built by Burla, da Cunha, Cavalcanti, Dobzhansky & Pavan (1950) at the Horto Florestal, near São Paulo. Each field consisted of 41 baited points spaced at 10 m. intervals and arranged in two lines 200 m. long intersecting in the middle at approximately right angles. At each baited point, about 1 kg. of fermenting banana was placed on the ground or on the fallen leaf cover. From time to time, at about 1 or 2 hr. intervals on the day of collecting, the flies that came to the bait were caught by sweeping with a cone-shaped collecting net in the air above the bait. Equal numbers of collections were made at all baits on the field, and, since several collectors participated in the work, every part of the field was taken care of by all collectors in rotation. This mitigated the disturbing influence of individual modes of collecting and made the numbers of flies caught on each bait reflect the density of the fly population in the vicinity of the baited point.

Collections were made on the same experimental field, i.e. with bait placed at the same 41 points, on 3 days, namely, on 29 December 1948, on 5 February and 11 June 1949. The total numbers of *Drosophila* flies caught on the field as a whole on these 3 days were respectively 1657, 1631, and 1452, and they belonged to at least 15, 12 and 14 different species. Among, these, species of the *willistoni* group (under this name are combined representatives of two sibling species, *D. willistoni* Sturtevant and *D. paulistorum* Dobzhansky & Pavan, that are difficult to distinguish morphologically) (see Burla *et al.* 1950), of the *medio-* group (comprising the species *D. mediostriata* Duda, *D. mediosignata* Dobzhansky & Pavan, and *D. mediopunctata* Dobzhansky & Pavan), and *D. capricorni* Dobzhansky & Pavan were common on all 3 collecting days. *D. guaramunu* Dobzhansky & Pavan and *D. griseolineata* Duda were common in December and February (145–162 individuals in each collection) but were rare in June (1–19 individuals). *D. polymorpha* Dobzhansky & Pavan was common in February (224), but rare in December (12) and June (7), and *D. bandeirantorum* Dobzhansky & Pavan was common in June (93), but not found at all in December and February.

The distribution on the experimental field of the *willistoni* and *medio-* groups, and of *D. griseolineata* Duda and *D. capricorni* Dobzhansky & Pavan is represented diagrammatically in Fig. 1. The diagrams are constructed as follows: the number of flies of a given species found on each of the 41 baits is expressed in percentage of the total number of the same species found on the whole field on the same day. The percentages are then symbolized by black columns of different heights which rest on a cross-shaped base representing the cross-shaped experimental field with its 41 baited points. Tall black columns signify, then, that a considerable proportion of individuals of a certain species were found at certain points on the field, and low columns signify that the species was rare on some of the baits. Each arm of the cross represents the distance of 100 m. between the centre of the experimental field and one of its four ends; eleven baited points are located on each arm. The numerical data for 29 December and 11 June are published in Burla *et al.* (1950).

The diagrams show that: (1) the distribution of the flies on the experimental field is far from uniform, nuclei of high and low density being formed; (2) the location of the nuclei of high density of one species may correspond to low density of other species; and (3) the distribution of the high and low densities on the field is not permanent but shifts from month to month. For example on 7 December, species of the *willistoni* group were frequent at the end of one of the arms of the cross-shaped field (the arm directed downward in Fig. 1); 100 individuals were caught on two baits, while only 25 individuals came to the seven baits on the opposite end of the field (the arm directed upward); 368 flies were caught on the whole field. On the same day, species of the *medio-* group showed high concentration at the centre of the field and along a different arm (directed to the left in Fig. 1). *D. griseolineata* was concentrated almost entirely in the central part of the field, while the baited points toward the ends of the arms attracted few or no individuals of the species.

By February 5th, the situation had changed radically. *D. willistoni* now showed high density in the central part of the field, while the arm which contained an aggregation of this species about 5 weeks earlier showed a rather low density. Species of the *medio-* group became relatively much less common than they had been in December and somewhat more uniformly distributed. *D. griseolineata* still showed high density in the central portion of the field, but now 44 out of a total of 145 individuals of this species were found at a single baited point (no. 13) which in December was not particularly well attended (4 out of 162 individuals). By June the situation altered again. *D. willistoni*, now less frequent relative to the *medio-* group, showed an aggregation along the arm

28 December 1948
5 February 1949
11 June 1949
willistoni group
medio- group
1 fly
griseolineata
cabricorni

Fig. 1.

of the cross directed to the right in Fig. 1. The species of the *medio-* group had a low density along the arm of the cross where they showed very high densities in December (directed downward in Fig. 1), but otherwise were distributed rather uniformly. *D. griseolineata* virtually disappeared—a single fly of this species was found on the field.

The data summarized in Fig. 1 are representative of a much larger body of data secured while collecting Drosophilae in various parts of Brazil by attracting them to banana bait. Over and over again it was observed that bait placed at points a dozen or so metres apart gives different assortments of species, the differences being unquestionably statistically significant. It was also noted that some species are more prone to form such local aggregations than others. Fig. 1 shows that *D. griseolineata* is concentrated at some baited points and wholly absent at others. *D. guaramunu* behaves similarly. *D. willistoni* and *medio-* groups tend to have more or less similar frequencies at neighbouring baited points (10 m. apart), but show non-uniformities at distances of the order of 20–40 m. *D. capricorni* was distributed relatively more evenly, although significant heterogeneities were present within 50–100 m. The degree of heterogeneity in *D. capricorni* is of the same order as found in the Californian *D. pseudoobscura*, while the behaviour of *D. willistoni* and *medio-* is about comparable to that of *D. melanogaster* and *D. funebris* as observed by Timoféeff-Ressovsky & Timoféeff-Ressovsky (1940) in Germany.

3. FOOD PREFERENCES

Two groups of factors must be considered in connexion with the microgeographic non-homogeneities in the spatial distribution of *Drosophila* species. The variety of species of trees is so large in tropical forests that if similar bait is placed at different points, some of the baited points are likely to be in the neighbourhood of trees in fruiting or flowering season, while others will be in places where natural food of *Drosophila* is scarce. More flies will be attracted to the bait in the former than in the latter places, and if different species of *Drosophila* have preferences for fruits, flowers, or sap of different trees, the relative frequencies of these species will vary from point to point. Furthermore, the flies may be sensitive to micro-environmental differences, such as more abundant moisture in depressions and relative dryness on slopes, or more light versus deeper shade depending upon the density of the vegetation. One might also suppose that representatives of each species of *Drosophila* could have an inherent tendency to aggregate in bands of conspecific individuals, but the experiments on release and recapture of marked flies in natural habitats indicate that no such tendency exists (Dobzhansky & Wright, 1943, 1947; Burla *et al.* 1950).

We have obtained evidence of food preferences in different species by making collections not on uniform, artificial bait but on natural bait of various kinds. From data of this type we are selecting three examples which illustrate the situation as it appeared in different parts of Brazil. On 6 April 1949, collecting was made at Baguassu, near Pirassununga, in the interior of the state of São Paulo. Samples were taken on fallen fruit of the macauba palm (*Acrocomia sclerocarpa*), and, about 40 m. away, on fallen flowers of a large *Bombax* tree; about a kilometre away, near a river, another sample was taken on fallen flowers of the same species of *Bombax*, and on artificial banana bait placed in the same neighbourhood. The results of the collecting are shown in Table 1. Macauba and banana fruits were clearly more attractive than *Bombax* flowers to *D. willistoni*, while *D. guarumunu* and species of the *medio-* group preferred the flowers. *D. campestris* (a new species of the *cardini* group) and *D. caponei* Pavan & Da Cunha occurred almost entirely on the flowers and ignored the fruits in the neighbourhood away from the river but were rare on the same species of flowers in the river neighbourhood. *D. willistoni* ignored *Bombax* almost entirely in the first, but not in the second, neighbourhood.

Table 1. *Percentages of various species of* Drosophila *in samples collected in two neighbourhoods near Pirassununga, São Paulo*

	Neighbourhood I		Neighbourhood II	
Species or group	Macauba fruits	*Bombax* flowers	*Bombax* flowers	Banana bait
willistoni	63·8	0·6	16·9	31·9
guaramunu	3·2	46·1	51·8	40·8
medio- group	11·7	22·6	20·3	11·5
campestris	0·9	22·9	1·7	0·9
polymorpha	7·1	0·5	7·6	11·9
calloptera group	7·1	—	—	0·3
bandeirantorum	0·1	—	1·2	2·0
caponei	—	5·7	—	—
Other species	6·1	1·6	0·4	0·7
Individuals collected	889	646	815	652

On 28–31 March 1949, collections were made on fallen fruits of various forest trees, and on artificial bait prepared from fermenting goiaba (*Psidium guayava*) fruit, in the vicinity of Park headquarters, Iguassú National Park, Paraná. Only common names of the trees were given by an experienced forest ranger; some of their scientific equivalents are, according to Dr George Black of the Instituto Agronomico do Norte, probably as follows: jaracatia = *Jacaratia* sp.; coquinho = a species of palm; canela amarela = *Nectandra grandiflora*; alecrim = *Marcetia* sp. (?);

Table 2. *Percentages of various species of* Drosophila *collected on different fruits at Iguassú National Park, Paraná*

Species or group	Jaracatia	Coquinho	Canela amarela	Aguahi	Alecrim	Cauna	Pitanga	Goiaba
willistoni	68·0	87·2	—	48·5	40·2	31·9	77·9	62·7
nebulosa	0·3	0·3	0·9	14·9	17·1	28·1	3·9	0·6
medio- group	20·3	1·6	16·4	11·1	4·9	5·0	3·9	1·8
guaramunu	3·0	5·0	81·9	17·2	23·5	32·6	14·3	6·4
polymorpha	8·3	6·0	0·9	8·4	14·3	2·1	—	28·3
Others	—	—	—	—	—	0·2	—	0·1
Individuals collected	300	367	116	586	286	427	154	3088

Table 3. *Percentages of various species of* Drosophila *collected on different fruits at the Instituto Agronomico do Norte, Belem do Pará*

	Terra Firme		Igapó						
Species or group	Banana bait	Bread-fruit	Banana bait	Bacaba	Murumurú	*Clusia* sp.	*Hura*	*Matisia*	*Lucuma*
willistoni group	79·2	64·0	58·1	15·0	40·9	56·7	12·6	92·3	75·9
fumipennis	11·1	—	2·0	—	—	20·0	1·0	—	11·8
nebulosa	0·3	—	3·0	—	0·7	—	0·5	—	—
simulans	—	—	0·1	—	4·7	—	—	—	—
sturtevanti	1·1	—	15·2	—	0·3	—	—	—	—
medio- group I	0·3	13·5	0·7	55·0	—	—	81·6	—	—
medio- group II	0·3	9·6	0·8	—	—	—	0·5	—	5·6
camargoi	6·7	6·1	6·6	5·0	—	—	—	6·7	—
fumosa	—	3·8	0·6	—	—	—	—	—	—
peruviana (?)	—	—	0·1	—	51·1	—	—	—	—
repleta group	—	0·4	6·0	—	1·8	—	—	0·4	0·3
canalinea	0·6	—	4·1	10·0	0·3	—	0·5	—	0·6
calloptera group	0·1	—	0·1	—	—	—	—	—	2·9
Others	1·7	2·6	2·7	15·0	—	23·4	3·2	0·7	2·3
Number of flies	360	261	712	40	276	30	191	284	341

cauna = *Ilex* sp. (?); pitanga = *Eugenia* sp. The data are summarized in Table 2. The commonest species in the region is *D. willistoni*, but it was conspicuously absent on canela amarela fruit. In another part of the forest, where a canela amarela tree stood near an alecrim tree, some *D. willistoni* were, however, present on the fruit of the former, thus showing that they are not completely unacceptable to this species. *D. nebulosa* preferred aguahi, alecrim and cauna fruits, while *D. polymorpha* chose the goiaba bait and alecrim fruit. Canela amarela was most acceptable to *D. guaramunu* and to a species of the *medio-* group.

Drosophila population samples were taken at various points in lowland ('igapó') and on higher ground ('terra firme') forests within 1–3 km. from the Instituto Agronomico do Norte, Belem do Pará, on 5–8 May 1949. Apart from artificial banana bait, we collected on fallen fruit of the breadfruit tree (*Artocarpus incisa*), bacaba palm (*Oenocarpus distichus*), murumurú palm (*Astrocaryum murumuru*), *Clusia* sp., *Hura crepitans*, *Matisia caudata* and *Lucuma* sp. We are greatly obliged to Dr George Black for naming these fruits. As many as 34 easily distinguishable species and species groups of *Drosophila* were found, several of them undescribed. An extract from the data is presented in Table 3. Species of the *willistoni* group (*willistoni* Sturtevant, *paulistorum* Dobzhansky & Pavan, *equinoxialis* Dobzhansky, and *tropicalis* Burla & da Cunha) were encountered in all samples, and in most cases constituted more than a half of all Drosophilae found. Fruits of *Hura crepitans*, of the bacaba palm, and of the breadfruit tree attracted an apparently undescribed species of the *medio-* group, which was rare or absent on other fruits. A species tentatively identified as *D. peruviana* Duda was common on the fruits of murumurú palm, although in June 1948, this species was found abundantly also on banana bait exposed in the same locality. *D. fumipennis* was fairly abundant on fruits of *Lucuma* and *Clusia*, and on banana bait, but rare on other fruits.

The food preferences exhibited by *Drosophila* species are, thus, not rigid. It is clear that different fruits attract different assortments of species of *Drosophila* in the same neighbourhood. But it is also

true that the same fruit may be visited by a given species in some but not in other neighbourhoods. Just what causes these variations in the attractiveness of the same kind of fruit is conjectural. Wagner (1944) has shown that the two closely related species, *D. mulleri* and *D. aldrichi*, have different nutritional requirements, so that strains of yeasts which satisfy one of these species may or may not be acceptable to the other. It is possible, then, that differences in the microfloras living on the same species of fruit in different neighbourhoods may be responsible for the different sets of *Drosophila* species which are attracted. The microclimatic conditions in which the fruits are placed are obviously another possible source of the variations. However that may be, it appears that most fruit-feeding species of *Drosophila* can, if necessary, subsist on many different kinds of fruit. Their ability to develop on standard laboratory culture media attests their rather omnivorous habits. Nevertheless, if choice is available, different Drosophilae do select different fruits, and some species are more and others less discriminating in their choices. The fungus-feeders are, of course, a different story: most of them do not come, or come rarely, to baits of fermenting fruits. We made no effort to collect the numerous fungus-feeding species, except when we saw them on fungi which abound in the humid interior of tropical rain forests. These collections are not included in the materials reported in this article.

4. SEASONAL CHANGES

Drosophila populations of temperate and cold lands are profoundly affected by radical changes in the natural environments produced by alternation of the seasons. By far the best data on seasonal changes in *Drosophila* populations are those of Patterson (1943) for the vicinity of Austin, Texas. Both absolute and relative abundance of species of *Drosophila* undergo cyclic changes with less striking variations from year to year. Some species have a sharp seasonal maximum and virtually disappear during some months; other species show 2- or even 3-yearly maxima, and can be collected at any time. The relative frequencies of different species change from month to month.

Contrary to the rather widespread misapprehension, seasonal changes are by no means lacking in the tropics. In most of Brazil, striking changes in the natural environment are caused by alternation of wet and dry seasons. In coastal rain forests and in parts of the Amazon basin, temperature and humidity are high enough throughout the year so that the inhabitants do not suffer from cold or desiccation. Nevertheless, different species of plants have different flowering and fruiting seasons and, accordingly, the environment is in a constant flux also for animals, whether fruit-feeding or not. Fixity of flowering and fruiting seasons occurs even in climates which are, from a purely meteorological standpoint, among the most constant on earth, e.g. the climate of the Espirito Santo Island, in the New Hebrides (Baker, 1947).

During 1948 and 1949, repeated collections of *Drosophila* were made at three collecting localities in the state of São Paulo, namely, at Vila Atlantica in the coastal rain forest, at Mogi das Cruzes on the plateau, and at Pirassununga in the interior. Care was taken to have the bait placed always at the same points, so that any differences in the relative frequencies of *Drosophila* species could not be ascribed to local variations in food distribution. The material collected was classified as a rule in the field with the aid of a binocular microscope. A summary of the data is presented in Table 4. The same table shows also the results of two collections made at Monjolinho, in the central part of the state of Goyaz, at the beginning of the rainy and of the dry seasons respectively. Also included are collections on banana bait made near the canal ('igarapé') Murutucú, on the grounds of the Instituto Agronomico do Norte, Belem, state of Pará, and, finally, the collections at Mogi das Cruzes made in 1946 and 1947. The latter collections were not necessarily made at the same points as the 1948–9 collections, although they were made certainly within the same neighbourhood. Seasonal changes near São Paulo (at Cantareira) have been discussed on pp. 2–4.

Table 4 shows that the relative frequencies of species of *Drosophila* in tropical climates undergo striking changes from month to month. Vila Atlantica, although located south of the Tropic of Capricorn, has a superhumid tropical climate. At Santos, some 20 km. to the east, the rainfall is above 100 mm. per month during the driest season (July and August), and between 200 and 300 mm. per month during the wettest season (January to March); the temperature means range from 18·6° (July) to 25·2° C. (February). The rainfall at Vila Atlantica is, if anything, more abundant than at Santos. Species of the *willistoni* group (*D. willistoni* and *D. paulistorum*) constituted about 77 % of the total *Drosophila* catch in January, but they were both absolutely and relatively less common (5–10 %) in August and September. Conversely, *D. capricorni* and species of the *medio-* group were common from August to November, and again in May and July, but rare in January and March. January and March saw an upsurge of the population of *D. fumipennis*, while September showed the highest observed frequencies of *D. sturtevanti* and *D. griseolineata*.

Mogi das Cruzes lies at about 850 m. above sea level, some 50 km. from the city of São Paulo. The monthly temperature means vary from 15° (June–August) to 21–22° C. (January–March), and precipitation varies from 30 mm. (July) to 208 mm. (January). As at Vila Atlantica, the species of the *willistoni* group

Table 4. *Seasonal changes in frequencies of species of* Drosophila

Locality and date	*willistoni* group	*capricorni* Dobzhansky & Pavan	*fumipennis* Duda	*bocainensis* Pavan & da Cunha	*nebulosa* Sturtevant	*simulans* group	*sturtevanti* Duda	*polymorpha* Dobzhansky & Pavan	*cardinoides* Dobzhansky & Pavan	*campestris* Pavan	*medio-* group	*bandeirantorum* Dobzhansky & Pavan	*immigrans* Sturtevant	*pallidipennis* Dobzhansky & Pavan	*griseolineata* Duda	*guarani* group	*guaramunu* Dobzhansky & Pavan	*fumosa* Pavan & da Cunha	*canalinea* Patterson & Mainland	*nigricruria* Patterson & Mainland	*repleta* groups	*nitrim* Dobzhansky & Pavan	Others	Nos. of species	Nos. of individuals
Vila Atlantica:																									
21–22. viii. 48	10·2	34·4	7·5	0·5	0·6	1·9	1·3	0·7	0·1	—	36·3	0·3	—	—	0·8	—	0·3	—	—	—	1·3	—	3·4	22	1106
26. ix. 48	5·0	10·1	10·9	0·03	—	3·6	17·5	1·0	—	—	29·2	1·1	0·2	—	9·3	0·3	—	0·3	—	—	0·5	—	2·0	19	3700
24. xi. 48	13·9	30·0	21·6	—	—	0·2	10·2	1·1	—	—	19·3	—	—	—	0·9	—	0·9	—	—	—	0·5	—	1·4	13	440
10. i. 49	77·3	0·3	18·1	—	0·01	1·3	1·0	1·3	—	—	0·4	0·03	—	—	0·05	0·03	0·1	—	—	—	—	—	0·1	14	6134
16. iii. 49	30·9	1·6	52·8	—	0·05	0·3	6·1	2·6	1·2	—	2·7	0·06	—	—	0·06	0·2	0·05	0·4	0·4	—	0·06	0·1	0·7	20	1592
27. v. 49	16·8	15·5	15·4	—	—	—	0·3	0·2	—	—	44·7	—	—	—	0·8	1·5	—	0·1	0·4	—	—	—	3·8	15	710
25. vii. 49	14·7	16·5	33·3	0·1	—	0·1	5·5	0·7	—	—	25·3	0·3	—	—	0·7	—	0·1	—	0·6	—	0·5	—	1·7	20	1058
1–16. ix. 46	1·3	0·5	—	—	—	14·6	0·3	1·0	0·9	—	51·1	9·6	6·4	—	0·5	1·8	0·4	—	—	—	4·6	—	8·1	17	769
15–16. xi. 46	12·8	3·4	—	0·4	—	11·7	2·3	—	0·4	—	43·6	5·6	—	—	4·9	10·6	1·9	—	—	0·8	1·5	—	0·4	15	266
11. v. 47	13·9	—	—	0·06	0·1	35·4	0·5	2·1	3·5	0·06	8·8	4·0	3·3	0·5	—	—	1·2	—	—	1·3	20·9	3·52	0·9	18	1732
14–28. xii. 47	36·8	—	—	0·1	1·2	0·6	0·3	21·6	0·03	—	25·9	2·4	0·5	—	1·1	0·2	7·4	—	0·03	—	0·5	0·1	0·5	20	3330
4. ix. 48	2·1	6·7	0·1	3·1	—	2·5	0·1	0·6	0·1	—	53·8	17·5	2·3	—	0·9	7·7	0·1	—	0·1	0·1	0·8	—	1·4	24	954
Mogi das Cruzes:																									
19. ix. 48	1·8	6·0	—	1·0	—	2·3	—	0·3	—	—	68·2	5·0	1·6	—	3·4	7·4	—	—	0·2	—	0·7	—	2·1	18	1028
24. x. 48	3·0	10·1	—	1·8	—	25·9	—	0·6	0·1	—	42·0	2·5	2·8	0·02	3·2	4·4	0·02	0·2	0·2	0·6	0·7	—	1·7	25	4473
17–26. xii. 48	20·8	15·1	1·1	1·0	0·4	6·0	0·05	1·9	—	—	18·5	3·2	2·0	0·04	15·8	1·1	6·4	—	0·2	—	0·8	—	0·5	23	2361
19–20. ii. 49	41·5	10·1	0·1	14·7	1·8	3·5	—	1·6	—	0·3	17·4	0·5	0·4	—	4·8	0·5	2·2	—	0·07	—	0·1	—	0·4	19	1399
22. v. 49	3·2	2·2	—	8·4	0·2	—	—	1·9	0·4	—	68·0	1·9	0·2	—	6·4	5·1	0·9	—	0·2	—	0·4	—	1·0	17	534
28. vi. 49	2·1	31·9	—	1·3	—	—	—	2·0	—	—	33·4	25·0	—	—	0·4	2·5	0·1	—	0·3	—	0·1	0·1	0·4	16	667
30. viii. 49	0·9	0·9	—	0·6	—	0·2	0·1	0·9	—	—	84·2	8·4	1·3	—	0·1	0·5	—	—	—	—	0·1	—	1·2	19	888
Pirassununga:																									
7. ix. 48	4·2	0·2	0·3	1·0	0·2	54·1	0·2	0·2	0·3	—	9·5	0·2	1·0	—	0·2	1·9	6·7	1·0	0·7	12·3	1·1	—	4·9	24	612
11. x. 48	2·2	0·04	—	0·3	0·9	69·6	0·04	1·5	—	—	2·8	0·4	1·2	0·2	—	0·2	18·5	0·04	0·3	0·04	0·4	—	1·5	22	2324
9. xii. 48	34·3	0·2	—	—	3·8	19·6	0·5	7·3	—	—	4·2	0·2	1·2	0·2	—	—	22·3	0·2	—	0·3	0·3	—	5·5	16	601
10. ii. 49	46·9	—	—	0·6	4·7	2·6	0·3	21·8	—	0·8	7·4	1·1	—	0·6	—	—	11·2	—	1·0	—	0·4	—	0·6	16	1605
6. iv. 49	50·1	0·5	0·3	—	0·5	—	1·0	9·0	—	0·9	12·0	0·9	—	0·2	—	—	19·0	—	0·2	—	—	0·2	5·9	18	1548
14. vi. 49	25·3	—	0·2	2·7	—	—	—	7·2	—	0·7	28·2	1·0	—	—	—	—	32·0	—	—	—	—	—	2·7	9	415
1. viii. 49	7·4	0·1	—	0·7	0·6	6·8	—	4·3	—	—	20·5	1·4	0·5	—	—	0·7	52·3	—	—	—	0·5	0·1	4·4	18	879
Monjolinho, Goyaz:																									
1–2. xi. 48	3·0	1·3	—	5·7	63·8	4·9	0·5	4·4	—	2·7	2·3	—	0·4	0·05	—	0·3	3·0	0·1	0·5	—	3·3	0·2	3·4	24	1950
7–10. vi. 49	21·1	3·0	4·5	0·9	5·2	6·3	7·8	0·1	—	0·5	21·9	—	0·1	0·06	—	1·8	11·4	0·2	0·1	0·1	8·5	1·4	4·6	28	1817
Belem:																									
1–10. vi. 48	76·3	0·2	—	—	0·4	0·3	4·7	0·5	0·1	—	1·0	—	—	—	—	0·9	—	0·2	0·3	—	0·5	1·9	12·6	26	16455
5. v. 49	58·1	—	2·0	—	3·0	0·1	15·1	0·3	0·6	—	1·5	—	—	0·1	—	0·1	—	0·9	4·1	—	4·8	0·1	10·0	26	713
17–28. vii. 49	54·2	—	0·9	—	0·1	—	7·9	7·9	0·1	—	5·6	—	—	—	—	0·2	—	—	0·1	—	3·5	15·7	3·8	22	1078
9–10. ix. 49	52·4	—	0·2	—	0·6	—	15·7	3·2	0·4	—	6·5	—	—	—	—	1·0	—	—	0·2	—	5·5	12·7	1·6	21	1092

showed highest frequencies during the warm and humid season (December–February), and underwent an eclipse during the cool and dry season (May–October). The *medio-* group of species showed the converse change, having been predominant (68 %) in September and May, and less frequent (17–19 %) in December and February. In contrast to Vila Atlantica, *D. capricorni* maintained rather high frequencies during the warm season (October–February), became rare in May, and turned out to be the commonest species in late June. *D. griseolineata* reached maximum expansion of its population at Mogi later (December) than at Vila Atlantica (September), and *D. fumipennis* and *D. sturtevanti* remained rare throughout. Instead, there occurred at Mogi brief outbursts of high frequencies of *D. bocainensis* (February), *D. simulans* Sturtevant (October), and *D. bandeirantorum* (September and June).

Pirassununga has dry (precipitation 21, 14 and 28 mm. in June, July and August respectively) but fairly warm winters (18·4–19·6° C.), and humid and warm summers (188 mm. precipitation and 23·5° mean temperature in January). The desiccation during the dry season is doubtless a limiting factor in the reproduction of *Drosophila* populations. As in the preceding two localities, the *D. willistoni* group (more than 90 % of individuals being *D. willistoni* and *D. paulistorum* less than 10 %) showed high frequencies during the wet and hot season and low ones during September and October. *D. simulans* showed a striking change from the status of the dominant species in September and October to an ostensible disappearance from April to June. The *medio-* group was fairly frequent from April to August and less so at other times. *D. guaramunu* was common at all times, and became predominant in June. *D. polymorpha*, *D. nigricruria* and *D. nebulosa* have each shown brief spurts of population growth.

The plateau of central Goyaz has fairly even temperature (monthly means from 18·3° to 22·6° C. at Santa Luzia) throughout the year, but has sharp dry seasons (10 mm. or less precipitation per month from June to August) and rainy seasons (242–321 mm. per month from November to March). Table 4 shows significant alterations of frequencies of several species between November 1948 and June 1949.

Belem lies in the superhumid equatorial zone. Here the mean temperature of the warmest month (26·8° C. in October) is 1·5° C. higher than that of the coolest (February), and the all-time high temperature record (36·6° C.) is 17·4° C. higher than the all-time low (19·2° C.). The precipitation varies from 72 mm. (November) to 402 mm. (March) per month, but the mean relative humidity changes only from 84 % (October) to 94 % (February). Nevertheless, our data show that the relative frequencies of *Drosophila* species are far from constant, except that the *D. willistoni* group remains predominant, and within that group the species *D. paulistorum* remains more frequent than *D. willistoni*, *D. tropicalis* Burla & da Cunha and *D. equinoxialis*, apparently in that order. Significant changes in abundance have been recorded for *D. nebulosa*, *D. fumipennis*, *D. sturtevanti*, *D. polymorpha*, *D. canalinea*, *D. mirim*, *D. peruviana* and *D. camargoi*.

Seasonal pulsations of population size occur in Brazilian Drosophilae, and there is no evidence that the amplitude of these pulsations is correlated with seasonal constancy or variability of the climate as evaluated on the basis of purely meteorological elements. To what extent the changes in the composition of *Drosophila* populations recorded in 1948–9 reflect the cyclic changes in the environment is an open question. Observations made at Mogi das Cruzes in 1946 and 1947 are relevant at this point (Table 4). *D. willistoni* was rare in September 1946, and common in December 1947; this agrees with the behaviour of this species group in 1948–9. But *D. capricorni* constituted 15 % of the total *Drosophila* population in December 1948, but was not recorded at all in December 1947. *D. simulans* was abundant in May 1947, but seemed to be absent in May 1949. *D. polymorpha* showed a high frequency in December 1947, and a low one in December 1948, while *D. griseolineata* did the opposite. Most striking of all are the high frequencies of *D. mirim* and of species of the *repleta* group recorded in May 1947; in 1948–9, these species never rose in frequency above 1 % of the total.

The meaning of these variations is in doubt since, as pointed out above, the 1946–7 samples at Mogi das Cruzes were not collected at exactly the same points as the 1948–9 samples. It may, however, be pointed out that Patterson (1943) recorded variations from year to year in seasonal abundance of some *Drosophila* species in the warm temperate climate of Texas. The numbers of sympatric species of *Drosophila* in most parts of Brazil is, however, greater than in Texas. This may create so complex a system of mutual relationships between the competing species that annual recurrence of the same set of relative frequencies may become improbable. In other words, climatic year-to-year variations may influence the complex tropical communities of *Drosophila* to a greater extent than they influence the relatively simpler communities in temperate countries.

5. COMMON AND RARE SPECIES

The variations in the abundance of *Drosophila* species in different neighbourhoods, on different foods, and at different times limit the value of any conclusions that we may reach regarding the commonness and rarity of species in a bioclimatic zone or a geographic

samples from the caatingas of Bahia it had frequencies in excess of 50% of the total; out of the 13 samples from the savanna of Rio Branco, *D. nebulosa* had frequencies above 50% in 8 samples, one of which had 686 flies, 683 of which were *D. nebulosa*. At Monjolinho, Goyaz, *D. nebulosa* was the most prevalent species in November 1948, but it held only the fifth place in frequency in June 1949, *D. willistoni* being the most frequent species at that time. In general, *D. willistoni* competes with *D. nebulosa* rather successfully in savanna environments, but surrenders to the latter the driest caatingas. Some of the food preferences of *D. nebulosa* are similar to those of *D. willistoni*. Thus, *D. nebulosa* was absent in the sugar-cane fermentation tank at Imperatriz, and rare on jaca fruits in Bahia, on marfim in Rio Branco, and on canela amarela at Iguassú, Paraná.

D. fumipennis is a member of the *willistoni* group in a broad sense, which includes in the Brazilian fauna, the four *willistoni*-like sibling species and also *D. capricorni*, *D. fumipennis*, *D. bocainensis* and *D. nebulosa*. *D. fumipennis* is the second most frequent species on Rio Negro and the third on the coast of São Paulo. It is also fairly common in Pará and in Acre. Its environmental preference thus seems to be for superhumid tropical climates, although it occurs occasionally even in the savannas of Rio Branco and in Goyaz. It has reached the status of dominant species in two samples from the coast of São Paulo, and in ten samples from Rio Negro. On Rio Negro it is quite abundant on some species of fruits and wholly absent on others. In May 1948, it was found in the vicinity of Belem on banana bait and on fruits of *Clusia* sp., *Hura crepitans* and *Lucuma* sp., but not on breadfruit, bacaba and murumurú palms or *Matisia* sp. (Table 3). *D. fumipennis* must be characterized as a common and ecologically fairly versatile species, but inferior in both respects to *D. willistoni* and *D. nebulosa*.

D. capricorni is a common species on the plateau and on the coast of São Paulo, where it reaches the status of the third and the fourth commonest species respectively. Elsewhere in Brazil it is rare, although a few individuals of this or a very similar species have been found even in the equatorial zone (forest of Rio Branco, Pará, Marahão) and in Goyaz. *D. bocainensis* is a widespread but usually infrequent species.

Except for the Bahian caatingas where they seem to be absent, species of the *medio-* group are, after those of the *willistoni* group, most widespread in Brazil. They hold the first place in abundance in the plateau region of São Paulo (*willistoni* being a close second), the second place in the forest of Rio Branco, in western Acre, and on the coast of São Paulo, and the third place in eastern Acre, in Goyaz, and in Rio Grande do Sul. It must be noted, however, that this group consists of at least eight morphologically rather similar species, at least four of them undescribed, and most or all breeding with difficulty on the standard banana agar laboratory medium. Our field notes show that, in contrast to the sibling species of the *willistoni* group, the species of the *medio-* group do not occur all together in the same samples, but are, on the contrary, ecologically well differentiated. A systematic revision of the group is needed before its ecology can be successfully studied. *D. guaramunu* has not been found at all in the nine of our regions closest to the Equator (Table 5), but it seems to be the dominant species or the second most frequent species in the southern part of Brazil: Rio Grande do Sul, central and western Paraná, and in the interior of São Paulo. It is fairly common on the plateau of São Paulo, and occurs on the coast of São Paulo and in central Goyaz. Table 1 and Table 2 show that it has food preferences of its own, different from those of *D. willistoni* and *D. nebulosa*. At Santo Angelo, Rio Grande do Sul, *D. guaramunu* was found predominant on pumpkin fields, while citrus fruits attracted relatively few of them. The nuclei of high population density of this species at Cantareira, near São Paulo, have been mentioned above (Fig. 1).

D. sturtevanti proved to be the commonest species on the island of Marajó, the second commonest in Pará, the third commonest in Maranhão, fairly common in the state of São Paulo, but not found at all in southern Brazil (Paraná and Rio Grande do Sul). Its food preferences include the jaca fruit (*Artocarpus integrifolia*) which is avoided by the *willistoni* group. In a fruit orchard at Palmares, territory of Acre, 666 of the 923 *Drosophila* caught on jaca were *D. sturtevanti* and there were no *willistoni*, while among the 300 flies collected on mango a few metres away only 53 were *sturtevanti* and 74 were *willistoni*. *D. sturtevanti* made up nearly 50% of the population of the sugar-cane juice fermenting tank at Imperatriz, Maranhão, which was also free of *willistoni*.

The *cardini* group contains *D. polymorpha*, *D. cardinoides*, *D. campestris* and *D. neocardini*. One or more of these species occur in every region and in almost every locality in Brazil where collection has been made. However, *D. polymorpha* and *D. cardinoides* are the only species of this group which occur in southern Brazil, and they are also commonest in Pará where all four species are recorded. But *D. campestris* is the commonest representative of the group in the drier regions—Goyaz, caatingas of Bahia, Maranhão, the interior of São Paulo, and, paradoxically, in Rio Negro (the Rio Negro form may be a different species).

D. simulans, and its much less common relative *D. melanogaster*, are in all probability not indigenous in Brazil. Nevertheless, *D. simulans* is widespread and is occasionally abundant in natural environments in places remote from human habitation. It is the most

Table 6. *Numbers of regions, localities, and samples in which certain species, or species groups of* Drosophila *held the first, second or third, or other frequency ranks*

Species or species group	Regions (17)				Localities (35)				Samples (156)			
	Most frequent	2nd or 3rd most frequent	Lower than 3rd place in frequency	Absent	Most frequent	2nd or 3rd most frequent	Lower than 3rd place in frequency	Absent	Most frequent	2nd or 3rd most frequent	Lower than 3rd place in frequency	Absent
willistoni group	9	6	2	—	13	18	4	—	67	48	23	18
fumipennis	—	2	6	9	3	3	11	18	12	23	23	98
capricorni	—	1	7	9	—	2	7	26	1	11	26	118
nebulosa	4	—	11	2	11	1	14	9	25	19	48	64
bocainensis	—	—	12	5	—	—	14	21	—	8	31	117
prosaltans Duda	—	1	7	9	—	2	10	23	—	5	21	130
sturtevanti	1	2	8	6	3	3	11	18	6	9	34	107
simulans group	—	4	10	3	—	6	13	16	5	18	28	105
ananassae Doleschall	—	—	4	13	—	—	4	31	—	2	6	148
polymorpha	—	2	11	4	—	2	15	18	—	16	55	85
cardinoides	—	2	11	4	—	2	15	18	—	9	31	116
neocardini Streisinger	—	—	4	13	—	—	5	30	—	—	10	146
campestris	—	1	10	6	—	3	18	14	—	19	38	99
guarani and *guaru* Dobzhansky & Pavan	—	—	11	6	—	—	16	19	2	6	36	112
guaramunu	2	2	3	10	2	3	4	26	9	13	25	109
griseolineata	—	—	5	12	—	—	6	29	—	2	20	134
bandeirantorum	—	—	5	12	—	—	6	29	—	3	27	126
immigrans	—	—	5	12			5	30	—	—	16	140
medio-group	1	6	9	1	3	13	13	6	27	60	37	32
fumosa	—	—	7	10	—	—	8	27	—	—	14	142
camargoi Dobzhansky & Pavan	—	—	5	12	—	—	7	28	—	5	10	141
dreyfusi Dobzhansky & Pavan	—	—	4	13		—	4	31	—	—	10	146
pallidipennis	—	—	5	12	—	—	5	30	—	—	13	143
canalinea group	—	1	9	7	—	1	11	23	—	2	31	123
repleta group	—	1	13	3	—	1	20	14	—	7	52	97
fulvimacula Paterson & Mainland	—	1	8	8	—	3	11	21	1	6	18	131
annulimana group	—	—	7	10	—	—	9	26	—	—	16	140
mirim	—	2	10	5	—	4	11	20	1	11	24	120
nigricruria	—	—	4	13	—	—	4	31	—	1	9	146
calloptera group	—	—	13	4	—	1	18	16	—	8	39	109

D. paulistorum during the warmer season. The other two species, *D. tropicalis* and *D. equinoxialis*, are known only from the basin of the Amazon, and thus their distribution regions are included in that of *D. paulistorum*. They are, as a rule, less common than either *D. willistoni* or *D. paulistorum*, except that in some samples taken in the north-eastern part of Marajó Island (Cape Maguarí) *D. tropicalis* and *D. willistoni* proved to be equally common and *D. paulistorum* rare. *D. willistoni* may, thus, be regarded ecologically the most versatile of *Drosophila* species in Brazil. *D. paulistorum* is superior to it only in some superhumid and hot climates (Pará, coast of São Paulo, close second on Rio Negro), while *D. nebulosa* forges ahead in savanna and caatinga environments.

D. nebulosa is the dominant species in four regions: savanna of Rio Branco, Maranhão, Goyaz, and the Bahian caatinga, in all of which it displaces *D. willistoni* to the second or the third place in frequency. It is significant that *D. nebulosa* is nowhere found to occupy the second or the third place in frequency; this species is dominant in regions which have a prolonged dry season, but in regions with a more even distribution of rainfall it rarely attains high abundance. The 11 localities and 22 out of the 25 samples in which *D. nebulosa* was the commonest species are in the four above-named regions. In 7 out of the 8

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D. sturtevanti proved to be the commonest species on the island of Marajó, the second commonest in Pará, the third commonest in Maranhão, fairly common in the state of São Paulo, but not found at all in southern Brazil (Paraná and Rio Grande do Sul). Its food preferences include the jaca fruit (*Artocarpus integrifolia*) which is avoided by the *willistoni* group. In a fruit orchard at Palmares, territory of Acre, 666 of the 923 *Drosophila* caught on jaca were *D. sturtevanti* and there were no *willistoni*, while among the 300 flies collected on mango a few metres away only 53 were *sturtevanti* and 74 were *willistoni*. *D. sturtevanti* made up nearly 50% of the population of the sugar-cane juice fermenting tank at Imperatriz, Maranhão, which was also free of *willistoni*.

The *cardini* group contains *D. polymorpha*, *D. cardinoides*, *D. campestris* and *D. neocardini*. One or more of these species occur in every region and in almost every locality in Brazil where collection has been made. However, *D. polymorpha* and *D. cardinoides* are the only species of this group which occur in southern Brazil, and they are also commonest in Pará where all four species are recorded. But *D. campestris* is the commonest representative of the group in the drier regions—Goyaz, caatingas of Bahia, Maranhão, the interior of São Paulo, and, paradoxically, in Rio Negro (the Rio Negro form may be a different species).

D. simulans, and its much less common relative *D. melanogaster*, are in all probability not indigenous in Brazil. Nevertheless, *D. simulans* is widespread and is occasionally abundant in natural environments in places remote from human habitation. It is the most

abundant, or the second most abundant, species in the interior and on the plateau of São Paulo during the cooler season. In Amazonia its distribution becomes spotty and confined to fruit orchards, in some of which it is, however, present in great numbers. *D. ananassae* is certainly an introduced species commonly found near human habitations but rare or absent in natural environments. In Amazonia it is the commonest household species. *D. mirim*, the smallest species of the genus in body size, is probably a native species which nevertheless thrives in the company of introduced scavengers (*D. simulans*, *D. melanogaster* and *D. ananassae*). In 20 of the 36 samples in which *D. mirim* was present, one or more of the scavenger species were present also.

The *calloptera* group contains *D. calloptera* Schiner and at least three other undescribed species. Although these species are attracted to banana bait they fail to develop on standard laboratory media. In natural habitats they occur especially on fruits and other vegetable remains in advanced stages of decomposition which are no longer very attractive to other Drosophilae. Thus, species of the *calloptera* group were found abundantly on old *Bertolettia excelsa* shells in Amazonian forests and on almost dried out babasú palm seeds (*Orbygnia* sp.) in Maranhão.

D. prosaltans is one of the rare species which occurs in many parts of Brazil, but usually is found in single specimens. It is, nevertheless, common in some localities, at least in some seasons. Most striking has been its presence as the second or third commonest species in five samples from the north-eastern part of Marajó Island, near Cape Maguarí. Other unusually good catches of *D. prosaltans* were made in some samples near Imperatriz, Maranhão, and in a narrowly circumscribed neighbourhood near Bertioga, on the coast of São Paulo. Banana bait several days old appears to be more attractive to this species than more freshly prepared bait.

6. SPECIES DIVERSITY

The amount of collecting in different parts of Brazil has been very unequal, and many species, especially in the equatorial zone, remain undescribed. Exact comparisons of numbers of species in tropical and temperate environments are, accordingly, impossible and only very general features of the situations can be discussed at present.

The 'caatingas' of Bahia showed the lowest species diversity among our seventeen regions of Brazil. Only five indigenous species (*nebulosa*, *pattersoni*, *cardinoides*, *mirim* and a member of the *repleta* group), and one presumably introduced one (*simulans*) were found common there, and eight additional species occurred rarely. The 'caatingas' are a semi-desert environment, where most plants lose leaves and become dormant during the prolonged dry season, which is beyond the toleration limit of most *Drosophila* species. Conversely, the rain forests of the equatorial zone offer a variety of habitats suitable for *Drosophila*; 38 species and species groups (not including collections on fungi) have been found in the vicinity of Belem, Pará. The records for other regions are intermediate between these extremes. About 20 species and species groups are found in most samples taken in the state of São Paulo (see Table 4), and about 30 are recorded in the aggregate of samples in each of the three collecting regions in that state.

The number of species in a sample depends not only upon the species diversity in the territory where the sample is taken but also on the size of the sample. Large samples are likely to include rare species absent in small ones, and hence a greater total number of species (Fisher, Corbet & Williams, 1943; Preston, 1948). Thus, Patterson (1943) found 47 species of the genus *Drosophila* among 673,020 individuals in the state of Texas, but only 20 species among 2253 flies from the neighbouring state of Oklahoma, 18 species among 4320 flies in Arkansas, and 21 species among 18,288 flies in Louisiana. The diversity of environments in which samples are taken in a given region evidently influences the observed species diversity. Among 141,126 individuals collected on an area about 30,000 sq.m. near Austin, Texas, Patterson (1943) records only 31 species in 233 samples taken from July 1938 to May 1941. His monthly collecting totals are from 45 to 23,619 flies and from 4 to 17 species. The samples from Brazilian localities recorded in Table 4 in this article contain from 266 to 16,455 flies and 9 to 28 species and species groups. Since a 'species group' may contain several species, it is fair to say that the species diversity in Brazil is at least twice as high as in Texas. This conclusion is strengthened if we recall that Brazilian records do not include most fungus-feeding species (the North-American fungus-feeding species seem to be, on the whole, more prone to come to banana bait than are many of the Brazilian fungus feeders).

7. DISCUSSION

Two or more species or varieties having identical ecological characteristics cannot coexist indefinitely in the same territory, because one of them will prove somewhat more efficient than the others, and will outbreed and supplant its weaker competitors. This principle, formulated by Gause (1934) and elaborated especially by Lack (1947), leads to the inference that sympatric species or strains either occupy different habitats within the same territory, or exploit the same habitat in different ways, which in the last analysis, amounts to the same thing: each form of life exploits some 'ecological niches', in at least one of which it

has a net superiority over all competitors. Presence of unoccupied or inefficiently exploited ecological niches constitutes a challenge to which organisms may respond by evolutionary changes that permit them to occupy these niches. To acquire and maintain a hold on a habitat, the occupant must possess a genotype the adaptive value of which in that habitat is superior to other genotypes. Different habitats require, however, different genotypes for most efficient exploitation. A multiplicity of habitats in a given territory makes possible coexistence of sympatric forms of life.

A variety of sympatric forms sufficient to exploit the opportunities offered by a territory may be engendered in the process of evolution in two ways. First, there may appear a group of related but distinct species, each adapted to control a single or a few habitats. Secondly, a species may develop adaptive polymorphism, and come to consist of a variety of interbreeding genotypes which possess highest adaptive values in different habitats. The first method will be advantageous if the genotypes which are adaptive in different habitats are so highly integrated systems of genes that Mendelian recombination in the hybrids leads to appearance of many adaptively inferior gene patterns. Reproductive isolation of the adaptive genotypes is then favoured by natural selection, and speciation is the result. The second method is advantageous when recombination leads to no loss of reproductive potential, and too rigid a fixation of adaptive genotypes reduces evolutionary plasticity.

Both methods of adaptation to environment containing a diversity of habitats have been used in evolution of *Drosophila*. The Brazilian fauna contains common, widespread, and nutritionally versatile species like *D. willistoni*, *D. nebulosa* and *D. paulistorum*. On the other hand, such species as *D. prosaltans*, *D. bandeirantorum*, *D. pallidipennis*, *D. fumosa*, *D. nigricruria*, and others, are common only in some environments or at some seasons. It has been shown in the present article that a community of sympatric species of *Drosophila* reacts to local and to seasonal variations in the environment by changes in the relative frequencies of constituent species. We hope to show in another publication that at least some of the species that are common and ecologically versatile possess elaborate systems of adaptive polymorphism; and that rare and specialized species tend to be relatively uniform genetically within a population of each locality, although they may show considerable geographic differentiation. Polymorphic species may react to environmental variations by adaptive changes in the relative frequencies of the constituent genotypes (Dobzhansky, 1949).

Biologically the most significant difference between tropical and temperate zone environments is that the former contain a greater diversity of adaptive niches than the latter. In response to this diversity, most groups of organisms are represented in tropical faunas and floras by greater numbers of species than in temperate or cold zone ones. Tropical environments present more numerous challenges to which organisms may respond by adaptive modifications than do temperate or cold zone environments. The diversification of organisms in the tropics is, in a way, a self-accelerating process, because the greater is the variety of organisms that live in a territory, the more complex becomes the environment and the more numerous are the challenges to which adaptive responses may be given.

8. ACKNOWLEDGEMENTS

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9. SUMMARY

1. Samples of *Drosophila* populations have been taken in 35 localities in 17 bioclimatic regions of Brazil. The techniques of collecting consisted in attracting the flies to bait of fermenting banana and procuring them on natural bait of fallen fruits, flowers, or other vegetable substances.

2. Samples taken at distances even as small as 10–20 m. from each other often contain different relative frequencies of various species of *Drosophila*. *Drosophila* populations thus form nuclei of high and low population densities. Some species tend to form discrete nuclei, and others to be distributed relatively more uniformly.

3. Species of *Drosophila* differ in food preferences, and some species are more specialized than others.

4. Repeated collecting within a locality discloses

the occurrence of changes in relative frequencies of different species from month to month. It is an open question to what extent these changes are cyclic and how regularly they are repeated in different years. Temporal changes occur both in regions in which dry seasons alternate with wet ones and in regions which have relatively uniform superhumid tropical climates.

5. Tropical faunas of *Drosophila* are richer in species than temperate or cold zone faunas. Within the tropics, rain forests have richer faunas than do more arid regions. The richness of tropical faunas and floras is considered to represent an adaptive response of the living matter to the diversity of habitats available in most tropical environments.

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THE SNOWSHOE RABBIT ENQUIRY, 1946–48

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(With 2 Figures in the Text)

1. INTRODUCTION

This report deals with fluctuations in numbers of the snowshoe rabbit, *Lepus americanus*, in 1946–7 and 1947–8. The collection and treatment of the material are described in reports for previous years (since 1931–2), where full acknowledgements are made to the co-operating organizations.

Snowshoe rabbits have an 8–11-year cycle in numbers throughout most of their range, but the cycle in one region may be wholly or partially out of phase with that in another. At the end of the period covered by the last published report, 1943–6, there was a scarcity of rabbits over almost the whole interior of Canada and the United States, following a sharp decline most generally noticeable in 1942–3, 1943–4 or 1944–5. However, in the Yukon, rabbits were abundant and at, or just past, their peak, and in Alaska they were approaching it. One year of recovery had been reported from the area between Lake Athabaska and Great Slave Lake and two years from the upper peninsula of Michigan and the Nelson River region of Manitoba; while in Nova Scotia and the New England States, where the 'crash' had been earliest (in 1940–1 on Cape Breton Island), recovery was well established and rabbits were becoming numerous again. There have thus been peak years somewhere on the continent in every year from 1939 to 1946, and, according to the present data, areas of local abundance were to be found in the Yukon and Alaska as late as 1947 and 1948. Nevertheless, as in past cycles, snowshoe rabbits reached peak densities at about the same time over a very considerable part of their range.

2. CANADA

(*a*) 1946–7

In 1946–7 approximately 62% of all observers in Canada still reported decrease or 'no change, not abundant'; but the area from which the beginnings of recovery were reported had become much greater, particularly in the middle west. This region now included the southern part of the Northwest Territories down to the junction of the Liard and Mackenzie Rivers, the northern half of Alberta, central and northern Saskatchewan and Manitoba east to the Nelson River and east shore of Lake Winnipeg. There were also a few reports of local increases in northern British Columbia and in a few places in north-western Ontario, but rabbits had continued to decline slightly elsewhere in these two regions and throughout Quebec as well.

The only striking decrease from previous abundance had occurred in the Yukon and the lower Mackenzie River valley. Even here the decline had not been catastrophic, for some observers who reported decrease stated that rabbits were still plentiful. Table 3, in which observers' replies have been grouped according to watersheds, shows the gradual progress and patchiness of the 'crash' which did not occur simultaneously throughout this far from homogeneous region, although over most of this area it appears that 1944–5 had been the peak year.

From the lower third of British Columbia reports of no change were again sent in by roughly half the observers. From a preliminary regional analysis of the whole series of reports, it seems that the rabbit populations in this area have shown no widespread regular fluctuations over the past 12 years. Another area in which there have been few pronounced changes is southern Ontario, including all the area south of a line from Sault Ste. Marie east to the Ottawa River. Here, while there had probably been a peak in the years 1942 or 1943, the subsequent 'crash' had been a minor one and rabbits had been neither very plentiful nor very scarce in this region since the end of the previous cycle in 1933–4.

In Nova Scotia, especially on Cape Breton Island, the cycle has been very definite with peaks in 1931–2 and 1939–41. Of the replies for 1946–7, 87% were of increase which had been both widespread and of considerable magnitude. Red foxes were said to be increasing as well.

The state of the rabbit cycle in New Brunswick was not very clear as no reports had been received from this province for 1945–6 and very few for the previous year. During 1946–7 rabbits seemed to have been fairly abundant in some places although there were many reports of no change.

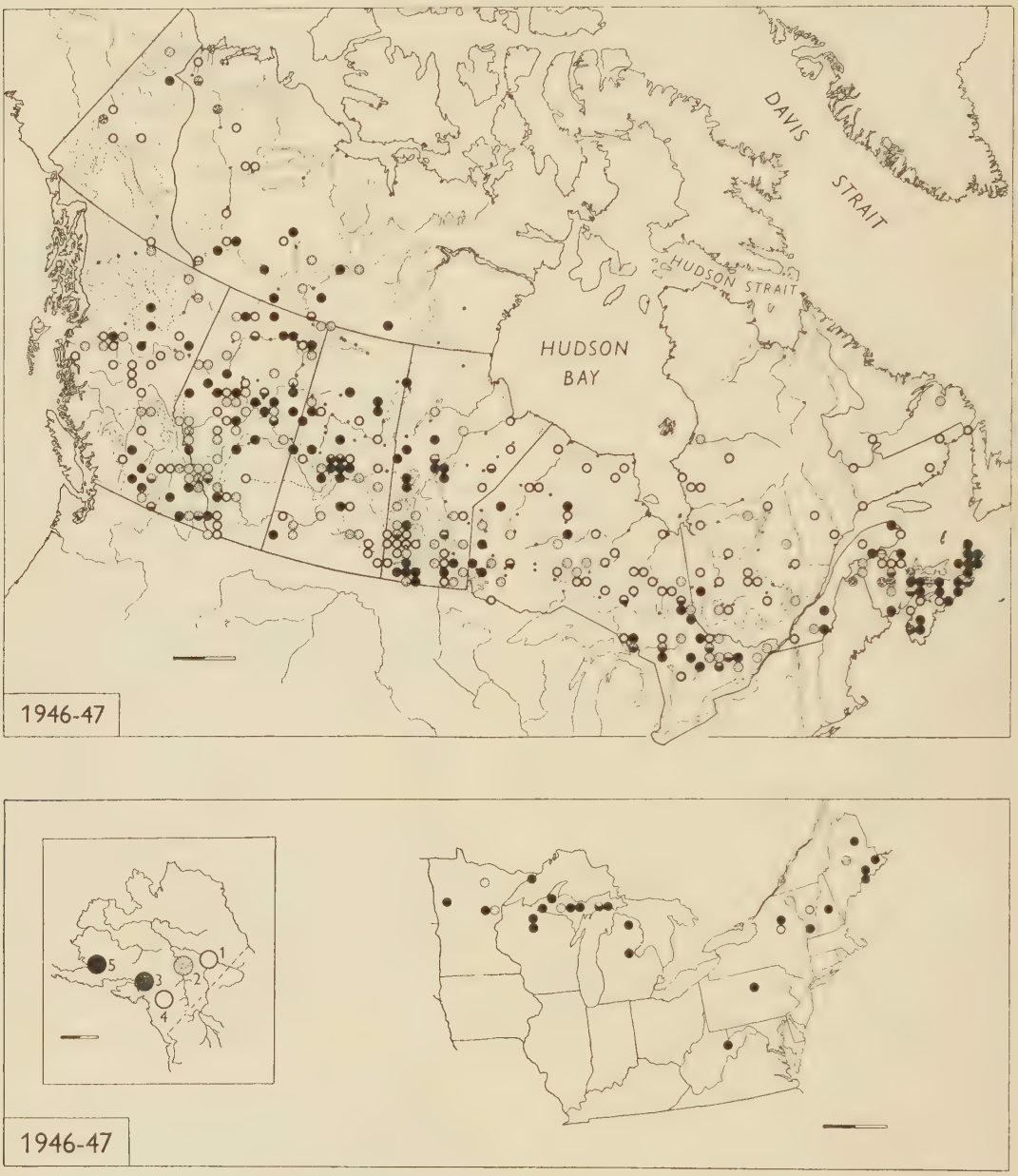

Fig. 1. **1946–47**. Reports about changes in abundance of snowshoe rabbits compared with 1945–46. Each circle of 30 miles diameter (100 miles in Alaska) marks the approximate centre of an area reported on by one or more observers. (For methods see *Canad. Field-Nat.* 54: 117.) Districts in Alaska: (1) Circle and (2) Fairbanks reported on by Mr J. W. Warwick; (3) Matanuska, Susitna and Yetna and (4) Copper River by Mr H. S. Larsen; (5) Bristol Bay by Mr C. M. Carson. Increase reports are shown black, decrease white, no change, abundant large irregular dots and all other no change stippled. Where reports at the same centre disagree the circle is divided up in proportion to the number of opinions of each kind. The total length of each scale represents 200 miles.

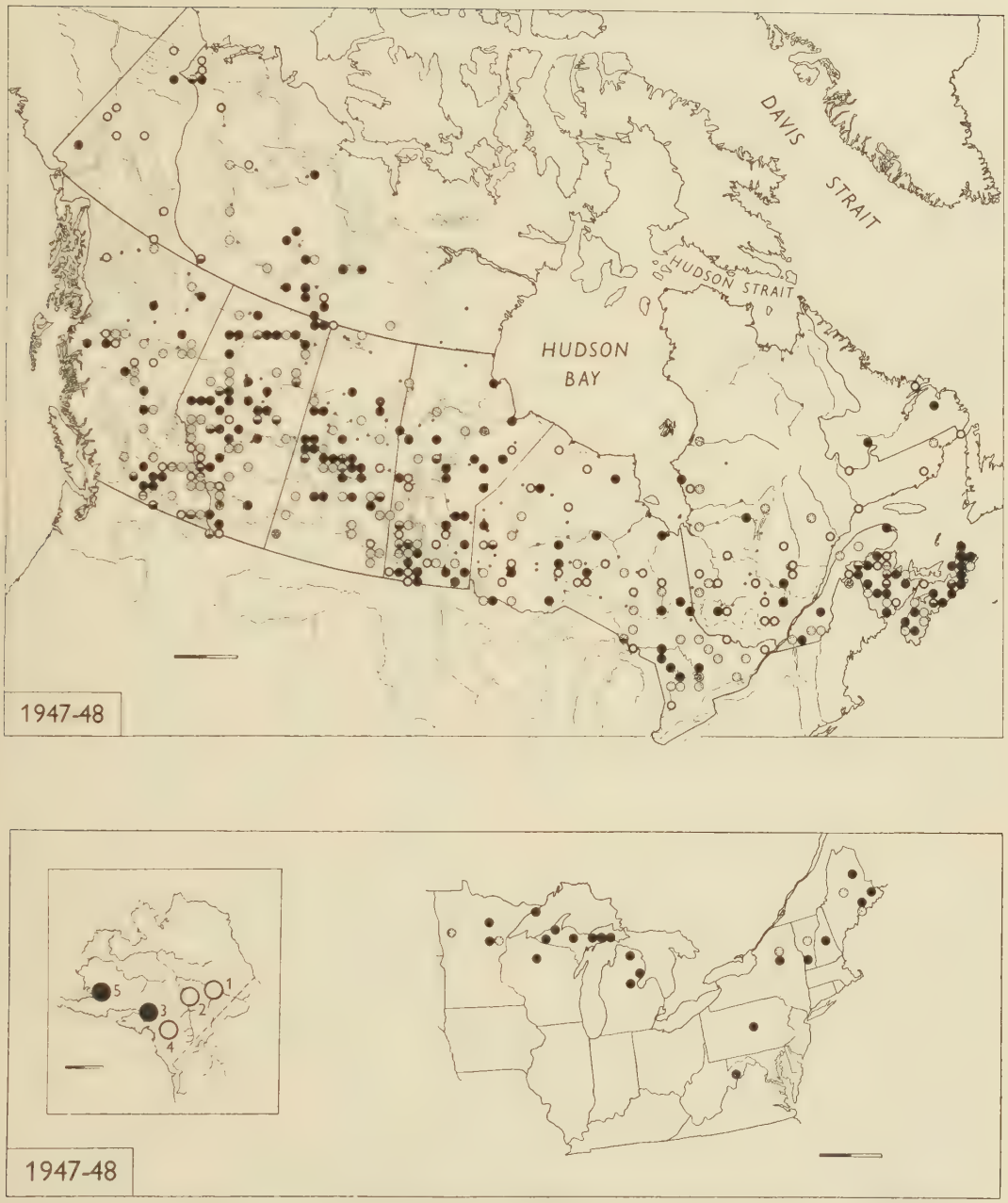

Fig. 2. **1947–48**. Reports about changes in abundance of snowshoe rabbits compared with 1946–47.

Table 1. *Reports about changes in abundance of snowshoe rabbits in Canada for the years* 1946–7, 1947–8, *each compared with the previous year (ending* 31 *May)*

	No. of observers							
	Increase		Decrease		No change		Total	
	1946–7	1947–8	1946–7	1947–8	1946–7	1947–8	1946–7	1947–8
Yukon	1	2	5	8	2	0	8	10
Northwest Territories	10	14	11	6	7	6	28	26
British Columbia	17	17	20	13	23	33	60	63
Alberta	30	40	16	6	38	34	84	80
Saskatchewan	21	31	11	4	12	26	44	61
Manitoba	23	36	20	11	16	17	59	64
Ontario	23	22	30	18	21	22	74	62
Quebec and Labrador	4	10	26	18	7	13	37	41
New Brunswick	8	14	4	6	12	8	24	28
Nova Scotia	24	24	3	2	3	7	30	33
Total	161	210	146	92	141	166	448	468

	Percentage of observers					
	Increase		Decrease		No change	
	1946–7	1947–8	1946–7	1947–8	1946–7	1947–8
Yukon	12·5	20	62·5	80	25	0
Northwest Territories	36	54	39	23	25	23
British Columbia	28·3	27	33·3	20·5	38·3	52·5
Alberta	36	50	19	7·5	45	42·5
Saskatchewan	48	51	25	6·5	27	42·5
Manitoba	39	56	34	17	27	27
Ontario	31	35·5	40·5	29	28·5	35·5
Quebec and Labrador	11	24·5	70	44	19	31·5
New Brunswick	33·3	50	16·7	21·5	50	28·5
Nova Scotia	80	73	10	6	10	21
Total	36	45	32·5	19·5	31·5	35·5

Table 2. *Reports about changes in abundance of snowshoe rabbits in U.S.A.* (Lepus americanus *only*) *for the years* 1946–7, 1947–8, *each compared with the previous year (ending* 31 *May)*

	No. of Observers							
	Increase		Decrease		No change		Total	
	1946–7	1947–8	1946–7	1947–8	1946–7	1947–8	1946–7	1947–8
Maine	4	3	0	0	1	2	5	5
Michigan	9	10	0	0	2	0	11	10
Minnesota	3	3	0	0	2	2	5	5
New Hampshire	1	1	0	0	0	0	1	1
New York	1	1	1	0	1	1	3	2
Pennsylvania	1	1	0	0	0	0	1	1
Vermont	1	1	1	0	0	1	2	2
West Virginia	1	1	0	0	0	0	1	1
Wisconsin	2	1	0	0	0	0	2	1
Total	23	22	2	0	6	6	31	28
Percentage	74	78·5	6·5	0	19·5	21·5		

Table 3. *Individual reports from the far north-west of Canada*

	1942–3	1943–4	1944–5	1945–6	1946–7	1947–8
Lower Liard, B.C.	—	—	N.	D.	N.s.	N.s.
Lower Liard, B.C.	N.	I.	N.	N.	D.	D.
Frances Lake, B.C.	I.	I.	I.a.	N.	—	D.
Whitehorse, Y.T.	I.	I.	I.	—	—	None seen
Mayo, Y.T.	I.	I.	I.	—	D.	D.
Selkirk, Y.T.	I.	I.	N.a.	N.a.	D.a.	D.
Selkirk, Y.T.	I.	I.	I.	D.	D.	D.
Stewart River, Y.T.	I.	I.a.	N.	D.a.	N.a.	D.
Dawson, Y.T.	N.	I.	I.	N.a.	D.a.*	D.
Old Crow, Y.T.	—	I.	N.a.	—	N.	D.
Ft. McPherson, N.W.T.	I.	D.	I.	N.	I.a.	(I.a.)†
Arctic Red River, N.W.T.	—	—	I.	—	N.	I.
Arctic Red River, N.W.T.	I.	I.	I.	I.	N.a.	—
Aklavik, N.W.T.	N.	N.	I.	D.	D.	D.
Aklavik, N.W.T.	I.	I.	N.	I.	D.	—
Delta, N.W.T.	I.	I.	I.	N.a.	D.	D.

I. = increase; D. = decrease; N. = no change; **a.** = abundant; s. = scarce; * = abundant in autumn;
† Near willow creeks in the foothills only, no rabbits in delta.

(*b*) 1947–8

The map for 1947–8 is very like the preceding one. The only change in the prairie provinces was a further extension of recovery eastwards to the Ontario border. The areas of reported increase now included almost all the prairie provinces and part of the Northwest Territories; the increase noted was generally very slight but in the spring of 1948 a few observers saw much greater numbers than for many years. At a few localities in northern Ontario and Quebec there were signs that rabbits were beginning to come back; in the far north-west (Table 3) there was said to be a general scarcity. On the eastern seaboard the increase had continued and rabbits were approaching peak proportions. On Cape Breton Island and the north-eastern mainland of Nova Scotia they were reported to be extremely plentiful and to have done considerable damage to saplings. In New Brunswick rabbits were generally abundant throughout most of the year, but two observers on opposite sides of the province noted a sudden decrease in January and February 1948.

3. THE UNITED STATES

Recovery was widespread during 1946–7 throughout the areas covered by this report, although it varied greatly in intensity. There was substantial increase in Michigan, Minnesota and Wisconsin, but rabbits were still not generally abundant, although some girdling damage was reported from Wisconsin. Only in parts of the upper peninsula of Michigan and in Maine and New Hampshire (where recovery had first been noticed), were rabbits becoming numerous. One observer in Maine estimated that the population had reached 60% of its previous peak level. The population over New York state as a whole showed a slight decrease in numbers (according to Mr R. W. Darrow, Supervisor of Game Research for the state) but the distribution was very patchy, some areas showing an increase, others remaining stationary or declining in numbers.

For 1947–8 no reports of decrease were received from any of the regions mapped. Recovery had become well established everywhere, but although the rabbit population was said to have doubled in some widely separated localities, the general opinion was that the density reached was not as high as had been expected.

4. ALASKA

Of the three observers who reported on natural snowshoe rabbit populations for the year 1946–7 two described different conditions in different parts of their territories. Mr J. W. Warwick, writing of an area 200 miles in radius around Fairbanks, reported no change except for a decline in the Circle District and along the Upper Yukon River. Mr H. S. Larsen in the same year observed small increases in the valleys of the Matanuska, Susitna and Yentna Rivers but a sharp decrease in the Copper River region, which latter he attributed to the extremely severe winter experienced in this district. However, as this and the other areas of decrease lie fairly close to the Yukon they may have been a part of the cyclical decline in this region. Farther west in the Bristol Bay drainage areas Mr C. M. Carson reported a 10–15% increase.

In 1947–8 a further decrease was noted in the same regions as before, and rabbits were now very scarce in the Copper River district. In the other areas rabbits were said to be much more numerous.

There were two reports about introduced snowshoe rabbits. On Kodiak and Afognak Islands, where the introduction was recent, a population seems to be establishing itself slowly. On Cap and Smeaton Islands, where snowshoe rabbits have had much longer to multiply, none has been seen, although it is believed a few are still there.

5. EPIDEMIC

There was no widespread epidemic among snowshoe rabbits during 1946–8 and only one observer each year reported that dead or dying rabbits had been found.

6. SUMMARY

1. For 1946–7 and 1947–8 reports have been analysed from 525 and 550 observers in Canada, the United States and Alaska.

2. By May 1948 recovery in snowshoe rabbits from the sharp decline in numbers in 1942–5 was widespread over most of the prairie provinces and the southern part of the Northwest Territories in Canada, and throughout that part of the United States included in this enquiry. The amount of increase had been small in most areas.

3. In the maritime provinces and the northern New England States rabbits became increasingly numerous during the two years and were nearing peak densities by the end of the period. Much damage had been done to small trees in some localities.

4. In the Yukon the cycle was in the downward phase, but the decline had been gradual and had not taken place at the same time throughout the area.

5. In Alaska rabbits had apparently not reached a peak in the two westerly areas, but in two areas near the Canadian border they had begun to disappear during 1946–7.

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TRACK MAKING BY MAN AND DOMESTIC ANIMALS

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(With 4 Figures in the Text)

1. INTRODUCTION

Footpaths made by man, and the tracks of domestic animals, are such commonplace things that they do not seem to have been considered worthy of attention by naturalists and other observers. Numerous writers have commented upon the tracks of wild animals, even though they have not made them the subject of investigation. Those of man and his domestic animals possess even more interesting features and they have proved to be just as puzzling in many respects. Furthermore, by observation upon the track-making habits of animals like the sheep, within the confines of a field, we may learn much about the behaviour of their wild relatives.

Man's tracks, or footpaths as they will be called hereafter, often mark some right of way, which may have existed for a length of time beyond living memory. They must obviously have objectives, at least one at each extremity, and yet even in the absence of obstacles they never take a straight line from one point to the other. We always tend to forget that the old and worn path which crosses a field, once had a beginning, and that someone blazed the trail. It may run the whole length of a long field or across a common, perhaps for half a mile and yet, apart from the meanderings of the path itself, it will not vary in width more than a foot or two. This is all the more remarkable when we consider that the stile which one sets out to reach may not be visible from that by which one enters the field.

2. THE MAKING OF A PATH

The reason for this absence of wandering by the traveller from a narrowly defined footpath remained a mystery to the author for many years. A singular opportunity arose, eventually, to study the making of a path by one person, who was quite oblivious of the fact that he was under observation. A gardener took up residence at a cottage about half a mile distant from the gardens at which he was employed. To reach his work he had to traverse an arable field and a permanent pasture. The latter being the park of a country mansion. In the arable field he was restricted, because of the crops, to walking alongside the hedge, but when he entered the park there was nothing to prevent any straying to right or to left. Although large trees and other landmarks may have provided a general direction, a slight rise in the ground made it impossible to see one side of the park from the other.

As one watched the man crossing the park, to and fro, twice daily, it was seen that he rarely looked up to take his bearings but generally trudged along, head down, with his eyes on the path. In using the path to guide him he was behaving in exactly the same way as do cows and sheep, but the latter phenomenon will be discussed later. There was nothing, so far, in these observations to suggest how he came to make this well-defined and narrow path in the first place.

It was not until there had been a heavy fall of snow which lay for several weeks, that certain facts came to light. He continued still to come to and fro across the park and he followed the footprints he had made on his first journey through the snow, until he had trodden out a well-defined path. This appeared to follow the same line as the old one in the grass. It was not until the snow had disappeared, however, that it was found that the snow footpath did not coincide exactly with the original grass footpath.

The old path, where it diverged, was still faintly visible. Had it been trodden by more than one man, it would have been the best defined of the two, but as it was not so, the user adopted the new path. Whether he would have done so if the deviation had been great, it is not possible to say.

It seems obvious that no definite path is taken in the first place, if the ground and the herbage are in such a condition that no mark is left. Such conditions prevail in dry weather when the grass is short and the soil is hard. As soon as the grass becomes long enough to be bruised and bent or when wet weather causes the user to leave soiled grass, then the path which is thus marked out, is adopted for subsequent use. Heavy use of a path by several persons will leave marks and changes in the herbage which will remain for a year or two after disuse.

It is by vision only that man strikes and maintains a path, at least so far as its general direction is concerned. Cows and sheep appear to rely on vision and not on scent.

3. THE WANDERINGS OF THE PATH

Footpaths and tracks are rarely straight, but ramble about in a seemingly aimless fashion. Several quite

untenable theories have been advanced to explain this phenomenon. There is the belief that man tends to walk in circles and that the variety of curves in a path are evidence of his constant attempts to change his direction. One may discount, too, the idea that 'the rolling English drunkard made the rolling English road'. Where obstacles such as tree stumps, rocks, or wet hollows lie on the straight line between two objectives, then men or animals will diverge to avoid them. It is apparently only ants that will labour to move an object such as a pebble, rather than go round it. Footpaths and tracks will still meander, however, in the absence of any such obstructions.

In the course of observations and inquiry into the possible reasons for this meandering, various phenomena were examined. It is well known that if a man walks across a field covered with snow or on a sandy seashore towards a definite point, that his path will exhibit twists and turns as evidenced by his footprints. The explanation is simple and is due to his striking zones of snow of different depths or sand of varying softness in a diagonal direction. The foot which encounters the increased resistance first, is slowed up, and the body is swung round to meet this resistance. When he happens to strike these zones at right angles, he continues straight through them without any deviation. This reaction is the same as that of waves of the sea, which on striking a beach diagonally, will swing round to become parallel to the beach.

There is evidence that differences in the hardness and softness of the ground do occur in wet weather and changes in herbage cause varying degrees of resistance to walking. That such factors may cause deviations from the direct line cannot be ignored, indeed they seem in a few cases to be the only explanation for deviations, but turns to left and right occur on many fields where the ground is uniformly hard and the herbage of uniform texture.

During investigations it was found that the deviations usually corresponded with rises and falls in the ground. Sometimes these irregularities of level escape notice, for it is surprising how insensitive is the eye to slight changes of level as compared with its acute sensitivity to lateral deviations. As in the examples quoted above, it is only when the path strikes the changes of level diagonally that there are changes of direction in the horizontal plane. If the approach is in the same direction as the change in level, the path will continue straight, whether it be uphill or downhill.

Fig. 1 shows deviations of the path already described, from the straight line from stile to gate across the park. The first deviation occurs between the points *A* and *B* on the line representing the footpath. It will be noted that this corresponds with a rise and fall in levels as shown in the upper part of the figure between the points *E* and *F*, on the line representing the levels of the footpath. There is a slight curve in the footpath between *B* and *C* and this corresponds with a slight rise and steep fall in the levels between *F* and *H*. In both cases the changes in level run obliquely across the footpath.

From the point *G*, on the line representing the levels of the footpath, to the gate, there is a steady fall in level over the whole length and this is at right angles to the path. The path should therefore take a straight line to the gate, but in actual fact it curves below the straight line between the point *D* and the gate, on the line representing the footpath, the whole slight curve being between *C* and the gate. This is explained by the fact that although the general fall is at right angles to the path, relics of a ridge and furrow system run obliquely across the path and these may be discerned in the slight rises and falls in level between the point *H* and the gate on the line representing the levels of the footpath.

Fig. 2 shows a section of another footpath reproduced in contour. The path runs straight from *A* to *B* and then turns directly downhill from *B* to *C* and further downhill from *C* to *D*. It then turns towards the right to run directly uphill from *D* to *E*. At *E* it swings left down the short hill to *F*.

So far the footpaths considered have met rises and falls in the ground diagonally or at right angles. There are cases where the direction of the path is almost but not quite in line with long hollows in the ground. Such an example is shown in Fig. 3. For the same reason as in the former examples, the feet will find the lowest level in the long hollow, and the tendency is, so far as the direction of the objective permits, to walk along the hollow. In Fig. 3 it will be noted that the path runs straight from *A* to *B* and then follows the hollow to *C*. At *C* it swings to the right uphill to *D*. Hollows in the ground may, if they are of the long narrow type, overlie fissures in the rock below. One is tempted to wonder whether some of the hollow-ways, which are not dead straight, have been initiated in this manner. Good examples of the type in mind are seen in the Selborne district of Hampshire.

It will be appreciated that the angle at which the direction of travel strikes a rise or fall in level will decide whether the path will follow a hollow or will turn to take the steepest direction up or down hill. On ground which is generally uneven, there will be a complexity of factors and in all cases which are difficult to explain, a detailed contour map will be necessary, both of the path and its surroundings. To take levels in the direction of the path only, may fail to explain its deviations from the straight line.

The reason why the feet turn straight uphill or downhill was not easy to discover. To walk diagonally up a hill may have the same effect in turning the body directly into the hill as happens when the wave strikes the shelving beach in the same oblique direction. The first foot to encounter the hill may be slowed up and the

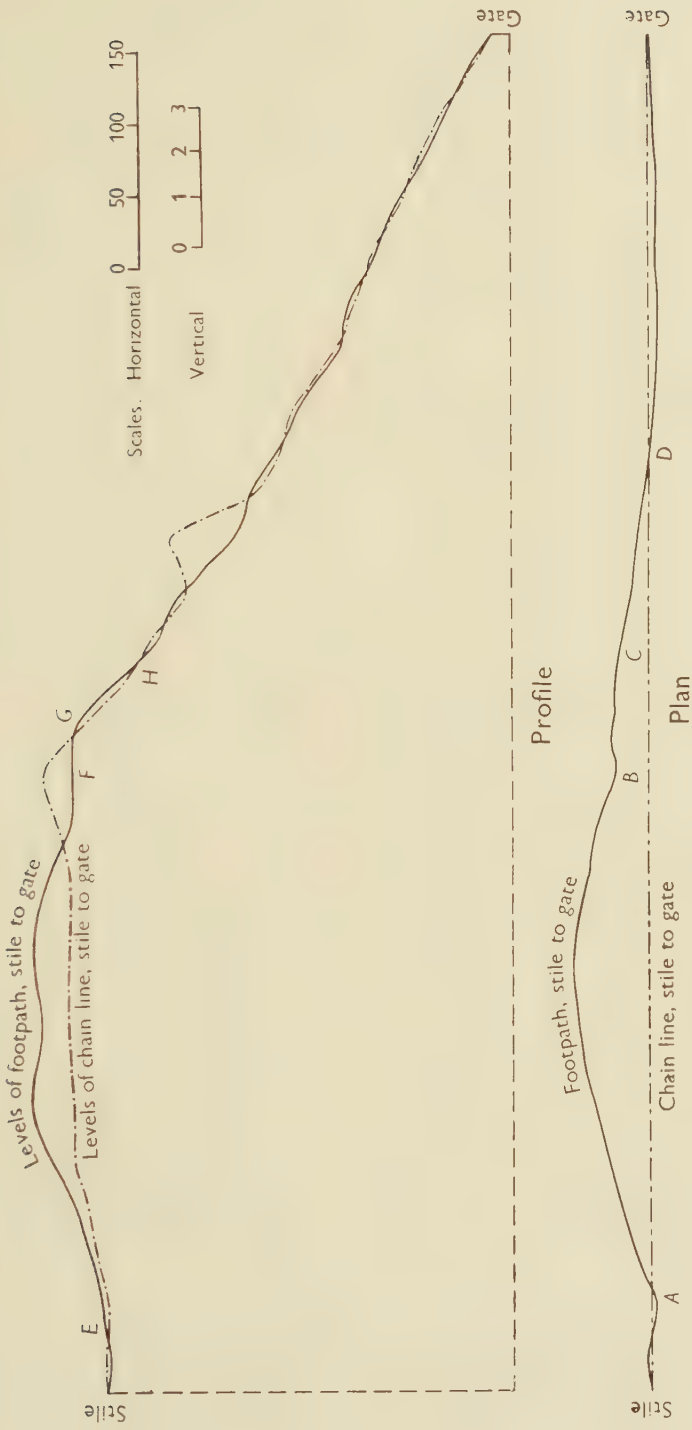

Fig. 1. Footpath in park. From stile (south-west corner) to field gate (north-east).

body swung round. This appears to be quite a sound argument until one comes to consider that it would not apply when walking diagonally downhill. The tendency would, according to this line of argument, be to turn the body back uphill. Many possible explanations were examined and rejected, for none would fit in with both the uphill and the downhill movement.

to lateral displacement of the body and our fine sense of balance compels us automatically and subconsciously to maintain the body in a vertical position, even on the slightest incline. Our ankle joints are articulated in such a manner as to allow only forward or backward inclination of the body. Any lateral movement causes acute pain. On experiencing the slightest feeling of strain or discomfort in the ankles

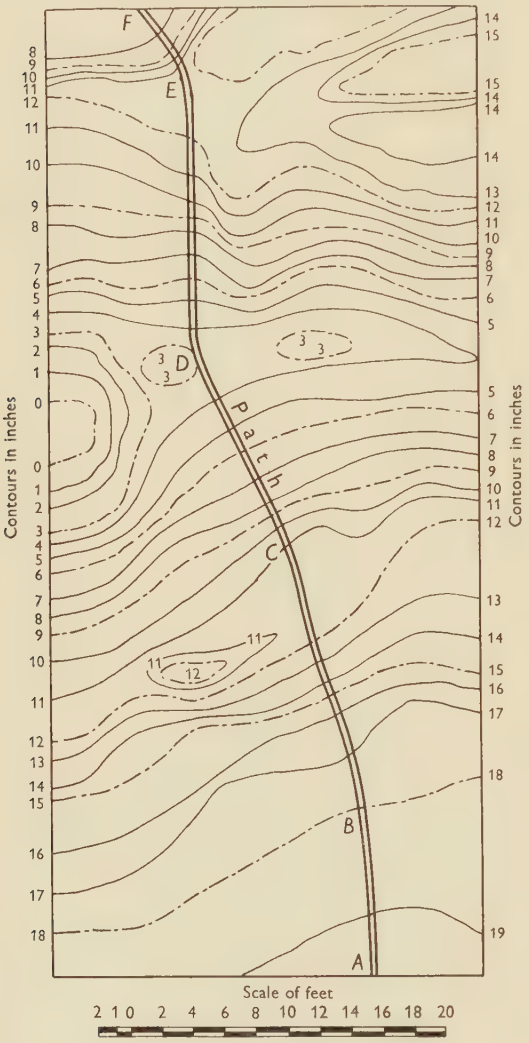

Fig. 2.

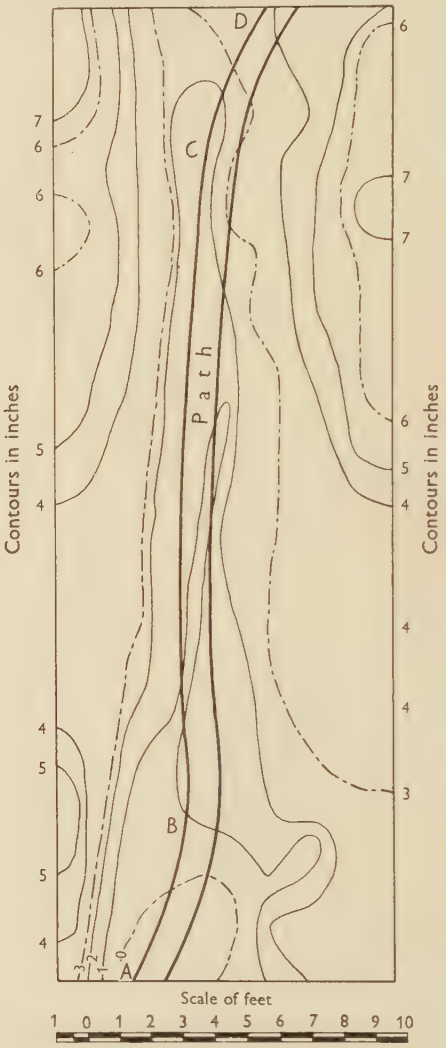

Fig. 3.

The true answer to the problem is found when one submits oneself to walking diagonally up or down a steep incline and then directly up or down. In the former cases there is a severe and painful strain on the ankle joints which is only relieved when one turns the feet directly up- or downhill. We are acutely sensitive we adjust our feet to give comfort and freedom from strain, while at the same time maintaining a vertical position of the body. This can only be done by turning directly up or down the incline. This reaction of the feet appears to be automatic and subconscious, just as is our adjustment of balance.

4. CATTLE AND SHEEP TRACKS

The tracks of cattle and sheep meander in the same way as do those of man, in response to rises and falls in the level of the ground.

Sheep will diverge from the straight line to avoid a patch of ground containing the stumps of cut thistles or other sharp vegetation and cattle may do the same. In one case, where sheep were forced to graze a field that had been badly infested with thistles, they developed sore feet and lips to such a severe extent that foot-and-mouth disease was suspected.

There is a very definite distinction, however, between the footpath of man and the tracks of these animals and it is to be found in the marginal vegetation. Footpaths have an indefinite margin and there is usually a distinct zonation of the component species of the turf. *Poa pratensis*, flanks the bare trodden centre of the path. This merges outwards into a zone of *Lolium perenne* and *Trifolium repens*. This zonation and the forces responsible for its development are described and discussed fully elsewhere (Bates, 1935). It is as well to mention, however, that the reason for this zonation is the fact that the degree of severity of treading decreases as the distance from the centre of the path increases. It is due also to the peculiar movement of the human foot as compared with the feet of animals. It is no simple up and down movement as it is with cows and sheep, nor is there the slight slipping that one sometimes gets with cows, nor do the feet of humans punch an impression in the ground as do hoofed animals. The human foot twists slightly with the sole of the shoe as a pivot, as the body moves forward. This imparts a grinding action.

Grasses such as *Agrostis* spp. and *Holcus mollis* whose growing points are above the soil surface are damaged and killed by this grinding by the foot. The species characteristic of the margins of the footpath, however, are adapted structurally to survive this injury, mainly because their growing points are just below ground level. These facts have been confirmed by direct experiments in which sown strips of the common grasses and wild white clover were subjected to treading (Bates, 1935).

It is found that the tracks of cattle and sheep are narrower than paths made by humans and they are a good deal more puddled in wet weather. The outstanding distinction is that the margins are sharply defined as compared with those of the footpath. They are quite clean cut and there is no gradual merging into the surrounds.

Although sheep tracks meander with rises and falls in the ground they do, on occasion, take a general direction diagonally up or down a steep hill, but it is found that the surface of the track is trodden into a terrace.

The so-called 'sheep terraces', however, found running horizontally in tiers along a hillside, are not caused by sheep, though they may be used by them on occasion. They are due to surface slip of the soil which produces cracks at intervals in the turf. The distance apart of these terraces differs with the slope, and where the hill face is indented, a complex system is set up. Many fine examples are seen from the train on a journey between Carlisle and Carstairs.

These terraces are discussed very fully by Darwin (1883), who examines the possibility of earthworms contributing to their formation. He rejects this idea and that of treading by sheep and quotes Prof. Henslow as having told Sir J. Hooker that he doubted the idea that sheep were the cause. Hooker quoted cases of these terraces on the Himalayan and Atlas ranges where there were no domesticated animals and few wild ones. Darwin concludes with the belief that the earth slips and cracks in horizontal lines transversely to the slope.

The author has seen these terraces on an old pit mound at Wellington in Shropshire, where no livestock have ever grazed. In another case at Dronfield in Derbyshire, a large area of a grass field subsided overnight, through the collapse of old mine workings. The area was fenced off immediately for the safety of livestock. A year later the steep slope on one side of the huge hollow had developed terraces.

The tracks made by cattle and sheep are usually 'outward bound' and lead to an objective such as a drinking place, a feeding crib, a salt lick, a separate pasture or even a communal resting place under a tree. The road back is never taken along the same track, unless it leads back to another definite objective.

When these animals are driven or if they stampede in fear they do not use a track. If they visit a feeding crib of their own free will, they journey along a track, but if they see the shepherd or stockman enter the field with a bag of corn, they will come running to him from all directions.

When cows are turned out into a field after milking, they are left to their own devices as soon as they have gone through the gate into the field where they are to graze. They will then follow a track, in single file, out into the field. When it is time for them to be driven up for the next milking and the cowman goes to bring them in, they will gather and come up in a bunch regardless of any tracks. One can satisfy oneself that many of the tracks are 'one way' by noting the direction of the footprints in the mud. When the grass is long, it is all bent in one direction.

These facts have been confirmed by Dr Fraser Darling (private communication), who has carried out observations on red deer in the Highlands, on sheep on North Rona and on the Soay sheep on St Kilda. Tracks, he states, are used by red deer in the Highlands when going somewhere, that somewhere usually being a change of pasturage, or trekking away

from oncoming snow down to a strath. The latter movement is not in the nature of a stampede, but is an orderly withdrawal. They may, however, go back the same way to higher ground, where they expect to find snow-free patches. A grazing return from low ground to high, does not involve the use of a track.

On North Rona, the sheep used to come on to the northern peninsula of chickweed during the evening, gradually, in twos or threes, and on no particular track, till they reached the neck of the peninsula, but in the early morning the trek back to the main body of the Island was *en masse* with much baa-ing, and they followed a diagonal track across the steep hill face.

Watching the Soay sheep on St Kilda he found that they used the tracks for changing grazing grounds and that the tracks might thus be used either way.

The track-making instinct in sheep

The following is an account of observations on track making by a flock of Clun sheep in Rodbaston Park, Staffordshire. The park has an even surface with a slight slope to the east, towards some swampy ground beyond a barbed wire fence (Fig. 4). A piece of land of 6 acres, together with the small swampy field below, was ploughed and reseeded direct in April 1944. The sheep were allowed access to the reseeded area from the day of sowing. The land was ploughed in an east to west direction by the ordinary method of setting up ridges (known as cops), at intervals of 30 yd. After the seed-bed had been prepared and the land heavily rolled, these ridges were hardly discernible. They were about 3 in. high along the central axis but sloped away gradually to the general level through a distance of about 18 in. on either side.

A severe drought occurred in early summer. The old turf provided little grazing, and on the newly seeded land the grass failed to appear and the earth was bare and dry. At the lower end of the field below the park, on the swampy ground, the grass grew luxuriantly and the sheep found access to this through three places in the barbed wire fence.

A curious phenomenon was noted in that the sheep made their way from the west end of the park and from the north side, by way of tracks made along the ridges and by no other way. The most remarkable fact was that they gathered from the north side on to ridge *a* which was contiguous with the old turf. It will be noted that on ridge *e*, the track diverted from the ridge at the point *x*. This was not with the object of taking a short cut to the gap in the fence, for at other points they had walked to the end of the ridge and then turned at right angles alongside the barbed wire fence to the other gap. It was because the ridge disappeared at this point *x*, and became a shallow hollow, owing to a fault in ploughing. After the sheep had passed through the barbed wire fence they made crooked tracks towards the swampy ground.

Later in the season the reseeded areas, as a whole, came into full production, but the swampy ground grew a large quantity of marsh horsetail and the grass became yellow through waterlogging. The sheep

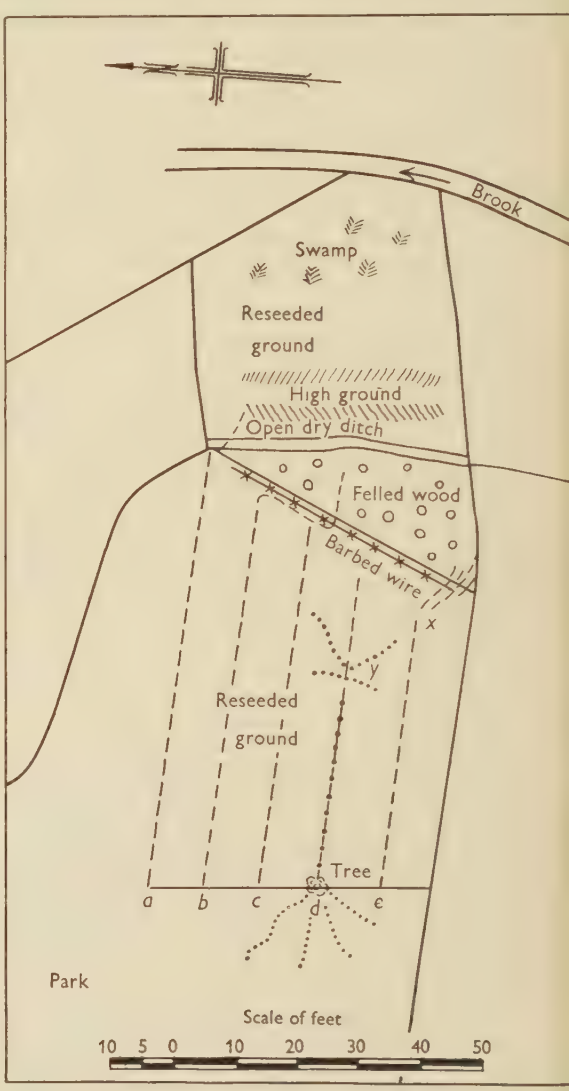

Fig. 4.

ceased to graze this part and the tracks became overgrown and obliterated.

During the heat of summer, the sheep lay under the oak tree at one end of ridge *d*. They approached by a definite track along the ridge, in this case coming from the opposite direction to that taken when seeking the swampy ground (dots in Fig. 4). The track com-

menced from a definite area *y* of about 4 sq. yd. of slightly elevated ground about 6 in. above the general level. A number of barely visible tracks converged upon it from all directions except the west. To the west side of the tree, the tracks leading to it from off the old turf came in several directions and were not straight.

The foregoing account shows in a most remarkable manner how sheep will follow a guiding line to an objective, rather than rely on direct sight of the objective or on scent or memory. The desire to follow a track seems to have been carried to a ridiculous extreme in the case of the resting ground under the tree, for this was only 117 yd. distant from the point of assembly at *y*. The ground was flat and the view unobstructed. The same sheep had no difficulty in seeing the shepherd with a bag of corn at three times this distance.

Ridges made by cows

One cannot fail to notice that, in some gateways and on parts of unmetalled roads trodden heavily by driven cows, the earth forms into ridges. These are broad and rounded in general appearance with fairly flat tops and steep sides. The furrows between them are deep and narrow. They look almost exactly as turnip ridges do after a heavy rolling. In summer, grass may grow on them and they may become temporarily stabilized. The first mention of this ridging effect, so far as can be discovered, is in the work of Vaughan Cornish (1914). It contains a photograph of a very typical example. He ascribes it to the cows placing their feet in exactly the same place every time they walk over the ground. On first consideration this explanation would appear to be the obvious one, but it does not bear close examination. It assumes that the cows all start from the same threshold line, and this is not the case. It assumes also that each cow takes care to follow in the steps of its leader. If one watches them either when they are driven or walking freely, they pay no attention to where they put their feet. It is only when on a very slippery slope or when they walk in fear that they tread warily.

The examination of a large number of examples revealed a condition which all of them had in common. It is only on a slope, however slight, that these ridges are formed. An opportunity arose to study the development of ridges in a gateway where they had formed and had been broken down by a cultivator, to level and reseed the ground. In autumn, the newly formed turf was broken up by the cows' hooves and the ground became puddled. Despite the fact that the cows trod in a random fashion and slithered about with their splay feet, the mud developed a formation of waves. The term 'wave' gives a better and more accurate description of their appearance than does the term 'ridge'. These waves were rough and irregular in shape. They are formed by the pushing or dragging of the mud downhill as the cows walk out into the field, or when they return. They are comparable to the ridges or ripples in sand or snow, the forces being the movement of the cows' feet and not water or wind. In this condition they bear little resemblance to their final form and in the author's investigation it was some time before the change took place. It happened as soon as the mud became dry, hard and stable. In this condition it was ground down by the hooves of the cows and the ridges became rounded and generally smooth.

If the stabilized ridges become slippery after a shower, the cows' feet will slip into the hollows and thus accentuate them. During prolonged wet weather the ridges may be broken down again. It seems that there is an optimum state of plasticity of the mud for wave formation, and also of hardness for grinding down into ridges.

5. RABBIT TRACKS

It has been suggested by many people that the rabbit, when using a track, puts its feet in the same place every time. The typical rabbit track is thought to be made up of a chain of equidistant depressions worn in the turf or on the bare ground. Each of these depressions is said to mark the spot where the hind feet and rear part of the body come down on to the ground.

This idea is much more feasible than that cows put their feet in the same place every time. The rabbit starts from the threshold of its burrow, where it pauses for a moment to survey the prospect. Further along the track, the spacing of the hops may be regulated possibly by a hole in the hedge, through which the rabbit has to squeeze or jump, and then start off again from a definite point.

Despite the probability of this regularity, observations and measurements show that there is no such thing. For considerable distances there may be a continuous track of almost uniform width. Following upon this there may be a chain of depressions, but upon examination it is found that these are not always equidistant nor are they always equal in size, either in width or length.

The fact that any track may be used by several rabbits of different sizes could account for this lack of uniformity in the depressions, both in respect of their area and their spacing. It does not account for the fact that there are these two types of track, the continuous and the chains of depressions.

A careful examination of the surface of the ground provides an explanation if one considers the normal gait of the rabbit when it is using its run as a means of reaching or returning from its feeding ground. Its pace is leisurely and one should not take into account

the comparatively rare occasions when the rabbit races home in fear, as having any effect in shaping the track. Jefferies (1896) has given an excellent description of the gait of the rabbit and has described it as almost a crawl. The long pointed hind feet are not raised very high from the ground and are almost dragged behind the fore feet. The latter are, incidentally, rarely put down together, but are spaced out.

From tracks in the snow and from watching a rabbit, one may obtain some idea of the mode of progression. The fore feet are placed on the ground and while they support the body the hind feet are brought forward with a slight spring, just clearing the ground, until they come to rest ahead of the place were the fore feet were planted. The latter have in the meantime been lifted. It seems that for a fraction of a second all the feet must be off the ground at the same time.

If one considers this movement of the hind feet, almost amounting to a crawl, it will be realized that any tangled or tall vegetation would catch the feet. On a close turf or on bare ground this would not occur and one will find that on such a surface there is a continuous track and no chain of depressions.

In soft tangled bent the rabbit takes a series of short hops because it is necessary to spring the hind feet clear of the obstructing soft grass. It is not often that a continuous track of uniform width persists for more than a few yards, and examination will reveal the reason. Continuity usually ends when obstruction is met in the form of a tuft of grass or rushes, a tangle of buttercup runners or perhaps a fallen twig.

6. ACKNOWLEDGEMENTS

The writer wishes to record his thanks to Dr F. Fraser Darling for help and advice, to Mr R. McD. Graham, of the Staffordshire Farm Institute, who carried out some of the surveying, and also to Mr F. Jepson, Deputy County Surveyor to the Staffordshire County Council, for the production of the figures.

7. SUMMARY

Permanent footpaths are made by man when a guiding line is provided by the marks of a previous passage. Footprints in snow, mud on the grass or bruising of the herbage provides a trail.

Meandering of the path may be due to changes from hard to soft ground or to variations in the composition of the herbage. It is due also to changes in the level of the ground. Man automatically adjusts his body to the vertical position and takes the direction up- or downhill which will cause the least strain on the ankle joints.

Cattle and sheep use a track only to reach some definite objective. Generally the return journey is not made along a track.

The so-called sheep terraces are caused by the earth slipping and cracking in horizontal lines transversely to the slope.

A case is described where sheep made tracks along ridges formed by ploughing, although these tracks were quite unnecessary as guides.

The ridges made by cows near gateways result from the formation of waves in the mud as it is pushed down the slope. The waves are subsequently rounded off by the grinding action of the cow's hooves when the mud dries.

Rabbit tracks are continuous when the turf is short but slight obstructions cause the rabbits to hop and the track then becomes a chain of depressions. The latter vary in size.

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NOTES ON THE ECOLOGY OF SHIP-FOULING ORGANISMS

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1. INTRODUCTION

One of the important aspects of the investigation of the fouling problem is the study of fouling organisms on the hulls of ships, and a number of accounts have been published of the kinds of animals which can settle and survive in this rigorous environment (e.g. Marine Corrosion Sub-Committee, 1944; Visscher, 1928). This study is not only important in establishing the extent to which ships enter dry-dock in a fouled condition and the degree to which they become fouled, but it can also yield, in favourable instances, useful indications of the incidence of fouling during the voyage. A brief account of the kind of results that can be obtained from analyses of fouling settlements has already been published (Bishop, Pyefinch & Spooner, 1949) and an account of the detailed results obtained from the examination of a large number of fouling samples will be published elsewhere. The purpose of the present paper is to present an account of certain aspects of the ecology of the more common fouling organisms. The subject is very much in its infancy and the paucity of material makes it necessary to present this account in the form of scattered notes, rather than as a connected sequence, but its presentation will, it is hoped, indicate the kind of information to be acquired if this study is to be taken further. Essentially, this information consists of an extension of our knowledge of the ecology and general biology of a number of common marine organisms which have a wide geographical range. Substantial contributions to this body of knowledge could be made by biologists who find themselves stationed, perhaps for other reasons, in the tropics or subtropics; and a realization of the wider use of observations, for example, on the growth rates and breeding of barnacles and tube-worms, may, it is hoped, stimulate inquiries along these lines. Such inquiries frequently do not require detailed knowledge or a special technical skill, but merely opportunities for continuous observations over periods of a year or more.

2. THE COMMON FOULING ORGANISMS

Though a considerable number of marine organisms have been recorded as occurring on ships, only a few of these occur with sufficient frequency to suggest that investigations of their general biology are likely to be useful. Among animal fouling organisms, barnacles, calcareous tube-worms and hydroids occur most frequently; oysters and encrusting Polyzoa are not uncommon, but of these only the two first mentioned seem likely to merit more detailed attention. The other forms mentioned are either so damaged or water-worn when the ship reaches dry-dock as to be difficult to identify and interpret (hydroids), or are so sensitive to the poisons commonly used in anti-fouling compositons as only to be able to settle when the latter is virtually non-toxic (encrusting Polyzoa, hydroids). In this paper, therefore, details will chiefly be given of aspects of the ecology of barnacles and tube-worms.

(*a*) *Barnacles*

(1) *Common species*

Barnacles are the most common and characteristic animal fouling organisms, and in the great majority of cases acorn barnacles are involved in these settlements, rather than stalked forms. In an extensive series of samples of ship fouling, 92% contained acorn barnacles, whereas only 6% contained pedunculate forms.

The species of acorn barnacle settling depends, of course, on the region in which the ship acquired its fouling. The barnacle fouling on ships dry-docking in this country after voyages in northern, temperate waters is principally *Balanus crenatus* Brug. and

B. improvisus Darwin, though *B. balanoides* (L.) occurs occasionally. Where fouling settlements have occurred in tropical or subtropical waters, *B. amphitrite* Darwin is the most common fouling form, though *B. tintinnabulum* Linn., is not uncommon and *B. improvisus* may sometimes be present.

Settlement of barnacles in northern temperate waters is seasonal in its incidence, though ships visiting ports in these waters at the appropriate season can become heavily fouled. *B. balanoides* settles only over a short period in the spring (chiefly in April), whereas the settlement of *B. crenatus* occurs, probably periodically, from April to September (Pyefinch, 1948). Some settlement of *B. improvisus* can also occur through the summer months. It is of interest to note the occurrence of *B. balanoides* as a fouling form, as it indicates that it is able to tolerate continuous immersion. In fact, growth of this species takes place more rapidly on the hull of a ship than in its normal intertidal environment, as individuals have been obtained in samples from ships operating in the Irish Sea that had attained a rostro-carinal diameter of 16–18 mm. within a year of settlement.

B. improvisus is, as is well known, markedly euryhaline, and it seems to be the characteristic barnacle settlement in such areas as the Baltic and in some of the estuaries of the east coast of this country.

Identification of the barnacles which settle in northern temperate waters usually presents few difficulties, but the full identification of tropical species is by no means so easy. Darwin (1854) described nine varieties of *B. amphitrite*, and this list has been more than doubled since. Further systematic work on this species is clearly needed, since varietal diagnosis within this species is complicated by the fact that some workers seem to have paid little attention to the work of their predecessors when describing, or re-describing, one of these varieties. Thus figures of the same variety drawn by two different workers may show differences greater than those often held to be characteristic of the varieties themselves. Many of the varieties are evidently very variable, but some seem to have more consistent characters than others and it has been found possible to distinguish specimens of *B. amphitrite* var. *communis* Darwin, var. *denticulata* Broch, var. *cirratus* Darwin and var. *stutsburi* Darwin with reasonable certainty. *B. amphitrite* var. *niveus* Darwin has also been recognized, but its identification is not always certain; this is one of the uncoloured varieties of *B. amphitrite* and it is therefore tempting, when examining a large sample of *B. amphitrite*, to refer uncoloured specimens of the species to this variety. For well-grown specimens this may be justified, but for smaller specimens it is not always safe, as some of the coloured varieties only acquire their colour slowly. Table 1 shows the incidence of colour among a population of small *B. amphitrite* which had settled on a population of larger *B. amphitrite communis*.

Table 1. *Colour of small specimens of* Balanus amphitrite.

Size group* (mm.)	Numbers			
	White	Part coloured	Coloured	Totals
1–2	7	5	0	12
2–3	3	12	10	25
3–4	1	19	18	38
4–5	0	5	16	21
5–6	0	1	2	3

* The dimension measured is rostro-carinal diameter.

This epizoic population was interpreted as a settlement of *B. a. communis*, but if only the smallest specimens had been available, the identity of the whole settlement would have been much more doubtful.

Some of the varieties of *B. amphitrite* have a restricted geographical distribution, e.g. var. *stutsburi* has only been recorded from the West African coast and var. *cirratus* has only been found, in the present survey, from ships which had probably become fouled in Australian ports or in ports in the Fiji islands, though its recorded range is rather wider; var. *denticulata* was first described by Broch (1927) from specimens taken from the Suez Canal, but Bishop (1950) has recently suggested that its range is rather wider and the results of the present survey indicate that its distribution, like that of *B. amphitrite communis*, is probably world-wide within tropical and subtropical regions.

B. tintinnabulum also has a large number of varieties, some of which do not appear to be readily identified, but only a few samples of this species were obtained from ships and these did not provide enough material to investigate the situation further.

One of the characteristic barnacles which settle on ships visiting Australian and New Zealand ports is *Elminius modestus* Darwin. Bishop (1947) has recently noted its appearance on the coast of Great Britain, and Crisp & Chipperfield (1948) have given further details of its distribution. It seems probable that this species has been brought to this country as a fouling form, since Bishop (1947) found living specimens on a ship which had sailed here direct from New Zealand. Knight Jones (1948) has pointed out the dangers created by its extensive settlement in estuaries. *E. modestus* now appears to be well established along the south coast, and is extending northwards both along the west (Purchon, 1948) and east (Knight Jones, 1948) coasts, and van der Meulen (1946) has recorded its presence in Holland. The general ecology

of this barnacle suggests that it may well become an important member of the intertidal community of our coasts and a characteristic ship-fouling form. Its dissemination is a good example of the effect of ship fouling in extending the range of a species.

(2) *Growth rate*

A number of studies have been made of the rate of growth of acorn barnacles. Hatton & Fischer-Piette (1932) and Moore (1934) have provided data for *Balanus balanoides*, Topsent (1911) and Pyefinch (1948) have given figures for *B. crenatus* and a number of records are also available for tropical species, e.g. Edmondson (1944) and Paul (1942) have given details of the rate of growth of *B. amphitrite*. One of the outstanding features of the growth of barnacles in tropical waters is its extreme rapidity in the period immediately following settlement. *B. amphitrite* reaches a rostro-carinal diameter of 14 mm. in 50 days at Pearl Harbour (Edmondson) and in Madras Harbour specimens of this species measured 8·8 mm. only 16 days after settlement (Paul). As *B. amphitrite* is not a large barnacle when fully grown, this growth rate soon decreases (thus Edmondson's figures suggest that the rostro-carinal diameter only increases 1 mm. during the third month after settlement). This rapid growth of tropical species immediately after settlement is important in ship-fouling studies, however, because it means that if settlement occurs within the first few days after a ship has arrived in port, the barnacles will be quite large before the ship leaves, if the stay is of the order of 2–3 weeks. Smith (1946) has shown that large barnacles may be able to survive a sea passage which is fatal to smaller individuals, so that this rapid growth is presumably an important factor in affecting the persistence of fouling on the hull.

In attempting to estimate, however, the time of settlement from a population of barnacles present on the hull of a ship when dry-docked, it is essential to know more than the growth rate determined for barnacles which have grown in an intertidal or sublittoral environment. Hatton & Fischer-Piette (1932) have shown that *B. balanoides* only grows, on the shore, for about 3 months in every year, whereas *B. crenatus* grows steadily throughout the summer months (Pyefinch, 1948) and it would seem likely that tropical species achieve their full stature uninterrupted by the effects of unfavourable environmental factors. Barnacles which settle on a ship, however, are exposed to an environment which at times closely resembles that of their contemporaries on more natural surfaces, but which at others is very different. When the ship puts to sea, the barnacles on the hull are exposed to an environment in which the quantity of food available is appreciably less than in inshore waters and in which it may be difficult, or impossible, for the barnacle to carry out its characteristic feeding reactions. Under the latter conditions, growth is not likely to take place rapidly. Evidence obtained in the course of the present studies suggests that the amount of growth which takes place at sea is negligible in comparison with that which takes place in port. For example, the hull of a ship which carried a settlement of *B. amphitrite communis* was examined in December 1947. Some of these barnacles had settled on the open surfaces of the plates, others had settled within the shelter of the butts between successive plates. Size distribution within the two populations was closely similar, and in both the modal group had a rostro-carinal diameter of 4–5 mm. Of the population of the plate faces, however, 88% were dead, whereas only 22% of the population sheltered by the butts had been killed. The shelter afforded by the latter environment had presumably been enough to allow survival of most of the population and the close similarity in size-group distribution in the two populations strongly suggests that no change had occurred in that near the plate butts during the passage back to this country. Death of most of those which had been more exposed may have been due to lack of food, as Smith (1946) has suggested, but the fact that the sheltered population had survived without growing suggests that food supply may not be a vital factor and that exposure to an open-sea environment may interfere with other vital processes, e.g. respiratory exchange.

(*b*) *Tube-worms*

(1) *Common species*

Identification of tube-worms from fouling samples often cannot be carried out completely, as many specimens are badly damaged as they are removed from the hull. Further, tube-worm settlements on ships often contain a high proportion of empty tubes (see § 3*c* below).

Species of the genus *Hydroides* are the most common calcareous tube-worms occurring as fouling organisms. *H. norvegica* Gunn, Mörch., which is world-wide in its distribution, is found most frequently, but specimens of *H. lunulifera* (Claparède) and *H. uncinata* (Philippi) have also been recorded. Other species of tube-worms have been much rarer in these samples. *Pomatoceros triqueter* (Mörch.) has occasionally been recorded in samples from ships which have operated in temperate waters, and other genera such as *Dasychone* and *Serpula* have been recorded in samples from ships which were heavily fouled. As the primary object of the investigation of fouling samples was the assessment of the efficiency of the anti-fouling composition, most attention was paid to the primary colonizers of the paint surface so

that secondary colonizers, such as *Dasychone* and *Serpula*, received less attention than perhaps they merited on other grounds.

(2) *Growth rate*

It has not proved possible to discover any extensive data on the growth rate of *Hydroides norvegica*. It is evident, however, that wide differences occur in temperate and tropical waters, since Bishop (unpublished results) has estimated that the tube of this species can reach a length of 40 mm. in 3 months in the Firth of Clyde, whereas Paul (1942) records that this tube length can be attained in 3 weeks in Madras Harbour. Further estimates from other points in the wide area of distribution of this species would be a valuable aid to estimates of settlement time.

More data are available for *Pomatoceros triqueter*. Dons (1926) found that the tube of this species grew at a rate of 1·3–1·5 mm. a month, but Fischer-Piette (1941) has recorded growth rates approximately five and four times as great as those for specimens measured at Port St Hubert and Dinard respectively. The average growth rates recorded by Bishop (unpublished results) in the Firth of Clyde are similar to those recorded by Fischer-Piette, but growth was faster during the summer (reaching a maximum of 12 mm. a month) and slower during the winter months (e.g. an average rate of 1·5 mm. a month for the period January–April inclusive).

(*c*) *Other forms*

Hydroids occur with some frequency on the hulls of ships, often being formed as epizoites on primary colonizers such as barnacles and tube-worms, but their usual condition when ships dry-dock is poor. Frequently only the stolon and the lower part of the hydrocaulus is left. Specific identification is always impossible and generic identification frequently so. Calyptoblast settlements are much more common than gymnoblast settlements, though heavy settlements of *Tubularia* (a genus which can survive exposure to moderate concentration of the poisons commonly used in anti-fouling compositions) have been noted occasionally, particularly on ships which have visited Bombay during January and February.

Polyzoa are also common fouling forms, most of the settlements being those of encrusting forms, which often spread over other colonizers, e.g. barnacles, tube-worms and oysters. Their condition in dry-dock is rarely such as to enable specific identification to be made; only the skeletal parts remain and the face of the zooecium is frequently so water-worn that the details of its form are missing. Branching forms (e.g. *Bugula*) have been recorded from a few samples and one set of samples consisted largely of huge masses of a foliaceous branching form allied to *Lepralia*.

Oysters are also commonly found in samples of fouling from ships which have become fouled in tropical ports. There is reason to suppose that these bivalves are very sensitive to heavy metal poisons such as copper and mercury and their settlement is therefore an indication that the anti-fouling composition has ceased to possess toxic properties.

This brief list does not, of course, include all the marine forms that have been encountered in this survey. Mussels, anemones, solitary and colonial ascidians and saddle-oysters have all been recorded and, if settlement has been sufficiently heavy, the community produced offers shelter to a number of errant forms, such as nereid worms. Heavy settlements of this degree of complexity are happily exceptional, since the resistance they offer to the passage of a ship through the water is considerable and this produces a marked effect both on speed and fuel consumption.

3. INTER-RELATIONSHIPS OF FOULING FORMS

(*a*) *Regional distribution on the hull*

The occurrence of a belt of algal settlement near the water-line, which is largely composed of *Enteromorpha* (though other algae such as *Ectocarpus* may also be present) is a well-known phenomenon. This, however, is the only really distinct example of any regional differences in distribution on the various parts of the hull. In these investigations, samples have usually been taken from the bottom flats below the bilge keels, from the side above the bilge keel and from near the water-line; an analysis of the occurrence of barnacles, tube-worms and oysters does not suggest that any of these fouling organisms are restricted to one level, though oysters were sometimes rather more common on the bottom flats and on the keel plate than on other parts of the hull. Possibly this is due to the fact that oyster larvae settle in greatest numbers on the under side of horizontal surfaces (Cole & Knight Jones, 1939). *Balanus balanoides* seems to occur most commonly near the water-line (and may occur at the water-line if the belt of algal settlement is absent), but this difference is not well marked.

(*b*) *Successive settlements*

The reconstruction of the fouling history of a voyage chiefly depends upon an analysis of the succession of settlement that has taken place and a very large proportion of the samples examined have provided instances of successive settlements. In interpreting such sequences, however, care must be exercised, since the settlement of one form may interfere with or prevent the settlement of latter

colonizers. The clearest example of such an interference effect is given by the water-line belt of algal fouling, where the dense settlement of filamentous algae probably prevents settlement of animal fouling organisms. Comparable effects may also occur between two types of animal fouling organisms, e.g. barnacle settlement does not seem to take place at all regularly upon a tube-worm settlement. Thus ships which have called at Mediterranean ports, where fouling due to *Hydroides norvegica* may be severe, do not become fouled to any great extent with barnacles, even if they visit ports (e.g. on the West African coasts) where these organisms usually settle in considerable numbers.

Further, there is some evidence that more subtle exclusion effects may occur. Analysis of one set of fouling samples indicated that primary colonization had been effected by *Balanus amphitrite communis* and *B. tintinnabulum*. Later, another settlement of the former had occurred, mostly epizoites, but this had chiefly taken place on *B. tintinnabulum* and not on the earlier settlement of *B. amphitrite communis*, since an average of 34·0 epizoites had settled on each specimen of *B. tintinnabulum*, whereas the average for *B. a. communis* was only 3·6. As *B. tintinnabulum* is much bigger than *B. amphitrite*, this difference might be due to the greater surface area presented by the former, but the difference is almost as striking if comparison is made between primary colonizers of comparable size, as under these circumstances the corresponding figures are 38·0 and 5·4. This suggests that other factors, such as possibly either the physical or the chemical characteristics of the surface provided by *B. tintinnabulum*, are important. Other observations have shown that the settlement of the cyprid larva can be markedly affected by such characteristics.

(*c*) *Death of fouling organisms*

Reference has already been made to the observation that hydroids and encrusting Polyzoa are almost invariably dead when collected from the hull of a ship in dry-dock and that the tubes of *Hydroides* spp. are often empty. It is reasonable to suppose, at least in the first two instances, that the animals have either been unable to survive the physical environment on the hull of a moving ship or have been unable to feed and so have died of starvation.

It is not uncommon to find a considerable proportion of other fouling forms such as barnacles dead and empty. In part, this may again be due to an inability to survive the rigorous environment on a moving ship, as Walton Smith (1946) has shown experimentally that small barnacles may be killed when rotated at speeds of up to 8 knots. The transition from warm tropical waters to temperate waters in the winter months is a further possible cause of death. The death of the majority of the members of a barnacle settlement has usually been attributed to a stay in a fresh-water port and if this deduction is indeed correct, it can be of great assistance in the reconstruction of a fouling history. Instances have occurred in which little doubt exists that a settlement has been killed by exposure to fresh water, but in many cases it is very doubtful if death has occurred from this cause. This difficulty could, it is suggested, be partly resolved if more were known of the survival of barnacles in diluted sea water or in fresh water and if more were known of the conditions prevailing in many estuarine ports. Species such as *Balanus improvisus* have long been known to be markedly euryhaline, and the records given by Fischer (1928) of the ranges of salinity that can be tolerated by *B. perforatus*, *B. crenatus* and *B. balanoides* suggests that these species share this property to some extent. Less information is available for the tropical species *B. amphitrite* and *B. tintinnabulum*, but varieties of the former occur in areas where considerable fluctuations of salinity exist and the occurrence of the latter on ships operating in the rivers of British Guiana (where the salinity is certainly very low) suggests that these species are also capable of surviving in diluted sea water. Short periods of immersion in completely fresh water may also be harmless, thus Cole (1932) has recorded that if *B. balanoides* is immersed in fresh water for 3½ days and is then replaced in sea water, the opercular valves open and the rate of cirral beat is normal within 5 hr. Ability to survive periods in fresh water may be correlated, to some extent, however, with size, since in laboratory experiments using *B. crenatus* ranging in rostro-carinal diameter from 1–2 to 14–16 mm., only specimens of diameter of more than 8 mm. survived immersion in fresh water for 3 days. Available evidence therefore suggests that members of a population of barnacles on a ship's hull should survive exposure to diluted sea water for short periods.

Survival is perhaps the more to be expected because many of the so-called fresh-water ports used by ocean-going vessels are not fully fresh water, or only present this condition for limited periods during the year. Further, the effect of this factor may not be equal for all depths on the hull, since for a ship of some draught, especially if loaded, the bottom flats may be in water which is appreciably more saline than areas of the hull near the water-line.

It seems probable that death of fouling organisms after settlement may be due to a number of causes, one or more of which may operate in any one instance. If a ship has been in completely fresh water for a week or more, the effects may be easily discernible, but where it has been in estuarine conditions, perhaps for a shorter period, the actual result may be the product of a number of factors. Many cases cannot be analysed

fully at present because of lack of knowledge of the factors concerned and of the mode of their interaction.

4. DISCUSSION

Many of the topics discussed in this paper emphasize the paucity of the available information on littoral and sublittoral marine conditions in many parts of the world. For many areas the littoral and sublittoral fauna is unknown and, though it is possible to deduce some of the commonest forms by the analysis of fouling samples from ships which seem likely to have become fouled in a given area at various seasons of the year, this is a clumsy and inaccurate substitute for direct observation. American workers (details in Bengough, 1943), have divided the oceans of the world into a series of ten zones, which represent grades of fouling intensity. Thus zones 1 and 2, comprising a world-wide belt running roughly 30° N. and 30° S. of the equator, represent the zone of greatest fouling intensity, whereas zones 9 and 10 (the Antarctic and Arctic seas) are the zones with the lowest fouling intensity. This grouping is valuable as a rough guide, but conditions vary widely from one port to another within a single zone, and a reasonably full and accurate interpretation of a series of fouling settlements depends upon a knowledge of conditions at or near individual ports.

Such knowledge would not only have an intrinsic value as a contribution to the stock of information on the biology of tropical marine animals, but it would eventually make a substantial contribution to the important economic problem of ship fouling. If the incidence of fouling, at various seasons of the year, were readily ascertainable, it would then become possible for the ship-owner to use an anti-fouling composition with properties best fitted to meet the conditions which would be encountered by the ship to which it was applied.

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6. SUMMARY

1. A brief description is given of the fouling organisms which occur on the hulls of ships, especially the animal fouling forms. Barnacles and tube-worms are those occurring most commonly. Hydroids and encrusting Polyzoa are also not uncommon, but are usually water-worn. Oysters are also common and, if settlement has been heavy, a complex community may develop which includes errant forms.

2. Certain aspects of the ecology of barnacles on a ship's hull are described, particularly their growth rates in this artificial environment. Data on the growth rates of tube-worms are summarized.

3. Examples of particular aspects of the ecology of animal fouling organisms include their regional distribution on the hull, successive settlements and the factors which may contribute to their death.

4. It is suggested that the accuracy of the interpretation of fouling samples could be increased considerably if more were known about the general biology of their constituent organisms. Studies of this nature, especially in tropical and subtropical waters, would therefore have an immediate practical application.

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THE FOOD OF FRESH-WATER STICKLEBACKS (*GASTEROSTEUS ACULEATUS* AND *PYGOSTEUS PUNGITIUS*), WITH A REVIEW OF METHODS USED IN STUDIES OF THE FOOD OF FISHES

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(With 1 Figure in the Text)

A. INTRODUCTION

The work on which this paper is based began as a study of the food of fresh-water stickleback (section C). In the course of this work it became desirable to review the methods in common use for studying the food of fishes (section B). It also became possible to study the food of roach from the stream in which most of the sticklebacks were collected, and so to examine the food of an entire community of fishes (section D). The various sections, which are closely inter-related, have been placed in their logical order, but some forward references have been unavoidable.

B. METHODS OF ASSESSMENT OF THE FOOD OF FRESH-WATER FISH

1. *Review of the literature*

Most workers studying the food of fresh-water fish have based their conclusions on study of the contents of the stomach or, more rarely, of the entire gut of captured fish. Digestion is less advanced in the stomach, and thus identification of the contents is usually more satisfactory. There has been great variety in the methods of analysing and presenting the data. Some authors (e.g. O'Donoghue & Boyd, 1930, 1932, 1934) have merely listed the food organisms found in each fish, but this, without analysis, gives no indication of the relative importance of each type of food organism, and most workers have analysed their data by one or more of the following methods.

(*a*) *The occurrence method.* The number of fish in which each food item occurs is listed as a percentage of the total number of fish examined (e.g. Allen, 1935; Frost, 1939, 1946*b*; Frost & Went, 1940; Hartley, 1940, 1947, 1948; and many others). Often the number of occurrences of all items is summed and scaled down to a percentage basis to show the percentage composition of the diet.

(*b*) *The number method.* The total numbers of individuals of each food item are given, and are also usually expressed as percentages of the total number of organisms found in all fish examined (e.g. Allen, 1938, 1941; Carpenter, 1940; Frost, 1939, 1946*b*; Frost & Went, 1940; Forbes, 1883; Neill, 1938; Radforth, 1940; and many others).

(*c*) *The dominance method.* The number of fish in which each food item occurs as the dominant foodstuff is expressed in one of the two ways used in the occurrence method (e.g. Southern, 1935; Frost, 1939; Frost & Went, 1940).

(*d*) *The volume and weight methods.* The volume or weight of each food item, or of the total food of each fish, is given, and is usually expressed as a percentage of the total weight of the fish (e.g. Allen, 1938; Blegvad, 1917; Frost, 1939; Radforth, 1940). Some authors (e.g. Neill, 1938; Ricker, 1937) calculate the weight of food eaten from the known average weight of each individual of each food item. Most workers use this method only to supplement some other method, and it is often used to show seasonal variation in food intake. Ricker, however, by counting and 'weighting' each type of food organism according to its known average weight, has evolved a method similar to the points method (below). McHugh (1940) used an extension of the volume method in which the percentage volume of the various food items was estimated by eye while the total was measured.

(*e*) *The fullness method.* Some workers wishing to demonstrate seasonal variation in food intake have used an arbitrary estimate of the fullness of the stomachs (Southern, 1935; Frost, 1939; Frost & Went, 1940; Hartley, 1947). This is only a special extension of the total volume method.

(*f*) *The points method.* Swynnerton & Worthington (1940) used a method in which the food items in each fish stomach were listed as common, frequent, etc., on the basis of rough counts and judgement by eye, due regard being taken of the size of the organisms as well as of their abundance (i.e. one large organism counted as much as a large number of small ones). Each category was then allotted a number of points and all the points gained by each food item were summed and scaled down to percentages, to give percentage composition of the food of all the fish

examined. This is essentially a volumetric method, and is similar in principle to those of Ricker and McHugh above. Until, however, dietetic values of food species are known, volume would appear to be a satisfactory basis for assessment, and this method has the advantage of being rapid. The points system of Swynnerton & Worthington was modified slightly by Frost (1943) by taking into account also the degree of fullness of the stomach; a modification followed by van Someren (1946).

Consideration of the various methods indicated that the points method was the most satisfactory and, with the slight modification described below, it was used for study of the food of stickleback (section C).

Facts in its favour are that it is rapid and easy, requires no special apparatus for measurement, is not influenced by frequent occurrence of a small organism in small numbers, nor of heavy bodies, like snail shells and caddis cases, and does not involve trying to count large numbers of small and broken organisms. It also does not give the spurious impression of accuracy which is given by some other methods.

Two criticisms of this method are offered. First, it is subjective, and the investigator may be influenced by prejudice in his allotment of points; but where large samples are analysed over a period of months this difficulty is to some extent overcome. It should also be realized that this criticism applies to all such work. In identifying the broken, and often partly digested, remains of organisms, ordinary taxonomical characters are usually obscured, and the investigator relies entirely on general facies. He is therefore equally liable to be influenced by prejudice, and the accuracy of his determinations depends on his knowledge of the food organisms. As most investigators of the food of fishes are people whose primary interest is in the fish themselves, rather than in the fauna and flora which form their food, it seems that great opportunity exists for such subjective inaccuracy. The same type of argument can be brought against counts of the numbers of organisms. Apart from the fact that unless great care is taken some food particles are not removed from the gut for examination, some at least of the organisms are normally broken, especially in those fishes which chew their food, and it is often only possible to estimate the number present; Smith (1947), for example, states that counts were made 'as far as possible'. This applies particularly to such important food organisms as copepods. Where plant tissue is involved counts become meaningless as well as inaccurate.

The second criticism is that the results given by the points method cannot be used for comparison with counts of the organisms in the habitat. Several workers (e.g. Neill, 1938), have compared the percentage by number of each food species in the fish with the percentage by number of the species present in samples of the fauna, and from this they have obtained data on the availability of food species and selection by the fish. Allen (1941, 1942) and Hess & Swartz (1941) have used the ratio of these percentages as a direct measure of the availability of each food species, which ratio they term the 'availability factor' and the 'forage ratio' respectively. They argue that, knowing these ratios for every member of the edible fauna, it is possible, on the basis of simple faunal counts, to discover what density of fish a given habitat is able to support, and they therefore claim that knowledge of these ratios is an important tool in fisheries research. Hess & Swartz suggest that percentage by weight or by volume, as well as by number, could be used for calculation of these ratios, and there seems no reason why the points method should not also be adapted for this purpose. In order to do this the percentage composition of the food eaten would be assessed on the guts by the points method, and the percentage composition of the fauna would be assessed, in much the same way, on a number of general collections, each of which would be treated much as if it were the contents of a fish gut. Consider any one species. Let the number of points gained by that species, expressed as a percentage of the total points gained by all species in all the collections, be a, and similarly let b be its corresponding percentage of the contents of the fish guts. Then the ratio $a:b$ would correspond to the forage ratio. Such a method would obviate the necessity of dealing with numerical samples of the fauna of areas of substratum, the validity of the results of which has been questioned by Mottley, Rainer & Rainwater (1939), and by Leonard (1939), who showed that such samples give little idea of the true percentage composition of the fauna, although they apparently do give a fair idea of the total volume of animals per unit area. This suggests that the area which it is usually possible to sample is too small to be uninfluenced by the patchy distribution of animals on the bottom. General collections made with a net or dredge would cover a much larger area than samples, and, although the collections would be less thorough, they should give a better idea of the true percentage composition of the fauna. They would also be much easier to make under difficult climatic conditions, and easier to assess on the return to the laboratory, as it would not be so necessary to find and count every organism. The points method would be both subjective and approximate, but it would avoid the unwarranted impression of accuracy which results from the use of counts of the organisms eaten and found in samples, which has led some authors, notably Allen, into basing a great deal of mathematical analysis on data which would appear to be fundamentally uncertain.

Unfortunately, in the present work the small size of the food organisms and the muddiness of the

habitat have made even a general relative assessment of the fauna on a points system impossible. It seems that no adequate estimate of availability of food species can be obtained for small fish living in very muddy places.

2. *Discussion*

The present investigation was designed to discover the percentage composition of the food of stickleback and its seasonal variation. Each stomach was assessed separately. The food species present were identified as far as possible and placed in their various food items, and then each food item was allotted 1, 2, 4, 8 or 16 points according to the volume of it present in the stomach. In this way one large organism counted as much as several small ones. In allotting the points the size of the fish and the fullness of the stomach were also taken into account, a full stomach, irrespective of the size of the fish, receiving a total of about 20 points, and a distended stomach receiving about 30.

The following examples should explain the system:

	Food species	Food item	Points allotted
Large fish, very full stomach	*Asellus* large, 2	Higher crustacea	16
	Cyclops, *c.* 100	Copepoda	8
	Chydorus, *c.* 50	Cladocera	2
		Total	26
Medium-sized fish, stomach quarter full	*Cyclops*, *c.* 10	Copepoda	2
	Chydorus, *c.* 20	Cladocera	2
	Rotifers, 8	Rotifera	1
		Total	5
Very small fish, stomach two-thirds full	*Cyclops*, 5	Copepoda	4
	Chydorus, 15	Cladocera	8
		Total	12

Table 1 shows the approximate points values of the most important food items in detail.

This method is essentially that of Frost (1943), except that there are more categories, which allowed of greater flexibility. The number of points allotted to each item was always 1, 2, 4, 8 or 16, and no intermediate values were given, as it was felt that in view of the approximation of the method too much flexibility was unnecessary. This has led to the difficulty that a stomach distended with one food item alone received only 16 points, and it is suggested that in future work it would be better to allot the points to the stomach in the first instance, and then to subdivide the number allotted to the various food items present. Dr W. E. Frost (in litt.) has also arrived, independently, at this conclusion, and has used the method in an investigation of the food of char. In the present investigation, however, the method used has given satisfactory service, as relatively few fish were found to have eaten only one food item, and large numbers of fish were examined. The main effect therefore of the rigidity in number of points allotted has been to make some common food items appear slightly less important than they actually were.

The data so obtained could be analysed both by the points and by the occurrence method, and dominance could be determined by counting only those occurrences allotted at least 8 points. In view of the differences in results which were expected from these three methods of analysis it was surprising to find that where large numbers of fish were assessed, and where the results were reduced to comparable percentage compositions of diet, the figures obtained from all three methods were almost identical, except that a few unimportant items were never dominant (Tables 7 and 10). Even with the relatively small samples from Windermere or Easdale the same similarity of results was observed (Table 7). Search was therefore made for published data which could be compared in the same manner. It was found that

Table 1. *This gives very approximately the numbers or amounts of those food items, forming* 3 % *or more of the food, which were necessary to gain* 8 *points in three sizes of* Gasterosteus aculeatus (*i.e. which would about, or a little less than, half fill the stomach*). *Twice as many or as much would have gained* 16 *points and half as many* 4 *and so on. Intermediate quantities were allotted* 1, 2, 4, 8 *or* 16 *points according to which value they most nearly approached*

Food item	Length of fish in mm. 20	40	60	Notes
Oligochaeta	Stomach nearly half full			Nearly always broken up
Sphaerium lacustre	½	1–2	*c.* 4–5	Exact number varied with size of mollusc. *Hydrobia* very variable
Hydrobia jenkinsi: large	½	1–2	*c.* 4–5	
small	*c.* 10	*c.* 20	*c.* 50	
Cladocera	*c.* 25	*c.* 50–70	*c.* 150–200	Figures refer to Chydoridae
Copepoda	Stomach nearly half full			Nearly always broken up
Ostracoda	*c.* 10	*c.* 20	*c.* 40	
Higher Crustacea: large	—	½–1	*c.* 1–2	Figures refer to *Asellus*, no. varied with size
small	*c.* 5	*c.* 10		
Chironomid larvae: large	—	*c.* 2	*c.* 4–5	Exact number varied with size of larvae
small	*c.* 5	*c.* 10	*c.* 20	
Chironomid pupae	*c.* ½–1	*c.* 2–3	*c.* 4–5	Rather variable in size
Diatoms and Detritus etc.	Stomach nearly half full			—

Table 2. *Figures recalculated from published data comparing three methods of assessing the percentage composition of the food of* 577 *brown trout* (*Frost*, 1939) *and* 192 *young salmon* (*Frost & Went*, 1940) *from the River Liffey, Ireland*

Fish species ...	*Salmo trutta*			Young *Salmo salar*		
	Composition of food (%)			Composition of food (%)		
Food item	Occurrence method	Dominance method	Number method	Occurrence method	Dominance method	Number method
Ephemeroptera winged	5·2	8·5	7·4	2·8	2·8	1·2
Ephemeroptera larvae	9·9	13·9	11·3	19·7	28·6	14·4
Plecoptera winged	3·1	2·4	1·4	1·1	.	0·2
Plecoptera larvae	7·0	21·4	11·7	3·0	.	0·2
Coleoptera winged	6·9	5·0	3·9	0·7	.	0·2
Coleoptera larvae	3·0	0·6	0·8	0·7	.	0·2
Diptera winged	8·0	10·5	19·8	5·5	1·8	1·2
Diptera pupae	3·0	0·8	3·0	6·9	12·0	16·4
Diptera larvae	5·1	2·6	2·5	3·0	0·9	0·7
Simulium pupae	1·8	0·6	1·4	3·9	3·7	4·9
Simulium larvae	5·9	3·0	8·2	12·4	21·2	21·7
Chironomid larvae	7·3	5·0	13·8	11·5	9·2	22·7
Trichoptera winged	2·7	0·8	0·9	0·9	1·8	0·5
Trichoptera pupae	1·5	0·2	0·4	2·5	.	0·7
Trichoptera larvae	11·7	15·9	9·5	18·3	13·8	12·4
Crustacea	2·2	3·0	+	2·8	0·9	0·2
Mollusca	1·3	.	+	1·8	0·9	0·7
Fish	0·6	2·4	+	0·1	0·9	0·2
Hemiptera (aquatic)	0·6	.	+	+	.	+
Hemiptera (terrest.)	3·0	1·0	2·0	0·5	.	0·2
Hymenoptera	4·1	0·6	2·0	.	.	.
Arachnida	2·5	.	+	0·7	.	0·2
Worms	0·8	1·4	+	0·5	1·8	0·2
Other organisms	2·4	0·6	+	0·9	.	0·2

Table 3. *Figures recalculated from Frost* (1946*b*) *comparing two methods of assessing the percentage composition of the food of* 106 *yellow eels* (Anguilla anguilla) *from Windermere*

	Composition of food (%)	
Food item	Occurrence method	Number method
Limnaea pereger	9·4	18·0
Valvata piscinalis	13·9	30·1
Pisidium/*Sphaerium*	16·1	22·2
Planorbis spp.	4·0	1·0
Ancylastrum fluviatile	0·4	0·1
Mollusca indet.	9·9	3·6
Leptocerid larvae	8·1	9·5
Polycentropid larvae	0·9	0·2
Phryganea sp. larvae	1·3	0·2
Trichopt. l. indet.	7·2	1·4
Sialis larvae	5·8	1·9
Ephemera danica nymphs	4·0	1·1
Leptophlebia sp. nymphs	0·9	0·4
Ecdyonurid nymphs	0·9	0·1
Odonata nymphs	0·9	0·1
Chironomid larvae	3·6	1·9
Gammarus pulex	9·4	7·3
Asellus	0·4	0·2
Oligochaeta	1·3	0·6
Perca	0·4	0·05
Others	0·9	0·1

Frost (1939) and Frost & Went (1940) have tables showing occurrence, dominance and number of organisms per fish, and that Frost (1946*b*) has a table showing number and occurrence. The methods had not been scaled down to comparable percentage compositions of diet. These have been calculated here (see Tables 2 and 3), when it emerges that here also different methods of assessment give substantially the same result. Radforth (1940) has similar tables, showing occurrence and number, from which it is possible to calculate the percentage composition of the diet of grayling (*Thymallus thymallus*) and flounder (*Platichthys flesus*), but here the agreement between the two different methods is less striking, probably because the tables are based on 50 fish only and there are many classes of food item.

There are grounds for stating that, for any fish with a generalized diet, provided a large number of specimens is examined, any of the commonly accepted methods of assessing the composition of the diet of fish from gut contents will give substantially the same result. Those food items important in the diet will always stand out clearly from those that are occasional or rare and so unimportant, and the variation between the different methods will probably not be greater than that between different samples of fish.

There remains, however, the special case of a fish

species which eats, amongst other organisms, large numbers of a particularly small species. Here use of the number method will distort the result. This is clearly shown by the results of Idyll with trout (1942), which have been recalculated as comparable percentage compositions of diet (Table 4). The trout had eaten large numbers of the small larvae of *Simulium* and this has resulted in distortion of the results obtained by the number method. This seems to be yet another reason why the number method should be rejected. It seems, therefore, that, although the volume or weight methods are probably the most satisfactory, the points method is a short cut to the same result and that the simpler occurrence or dominance methods are likely to give the same result as the points method.

This should be of particular value in investigations of the food of fish like Cyprinidae which chew their food (Hartley, 1947) and so make counting impossible. The presence of large volumes of mucus in some species prevents accurate measurement of weight or volume and this, coupled with the elongate U-shape of the stomach of some fish (e.g. Cyprinidae), makes allocation of points difficult. The investigator can therefore only use the occurrence method, which although apparently the least satisfactory is now shown to give substantially the same results as theoretically better methods.

In the present investigation the food of the roach (see section D) was assessed by the occurrence method for the reasons given above.

C. THE FOOD OF FRESH-WATER STICKLEBACKS (*GASTEROSTEUS ACULEATUS* L. AND *PYGOSTEUS PUNGITIUS* (L.))

Fresh-water sticklebacks are common and widely distributed throughout Europe (Bertin, 1925), but it appears that little is known of their ecology. Brief descriptions of their habits and food occur in several books on fishes, and they have frequently been used as laboratory animals for study of morphology, physiology, toxicology, etc. Detailed study of these fish has been undertaken by comparatively few authors, and most of these have concerned themselves with such subjects as osmo-regulation, embryology, physiology of secondary sexual characters, breeding habits and behaviour, taxonomy and evolution.

In view of this lack of ecological knowledge, Dr J. W. Jones and I decided to make a field study of both European species of fresh-water stickleback. This paper is the first of two, the second of which will deal with age and growth.

1. *Sources of material*

All the ten-spined (*Pygosteus pungitius*) and most of the three-spined sticklebacks (*Gasterosteus aculeatus*)

Table 4. *The percentage composition of the food assessed by two methods of the rainbow trout* (Salmo gairdneri) *and the cutthroat trout* (S. clarkii) *of the Cowichan River System, British Columbia. Data recalculated from Idyll* (1942)

Species of fish	...	*Salmo gairdneri*		*Salmo clarkii*	
Number of fish	...	220		120	
Method of Assessment	...	Occurrence	Number	Occurrence	Number
Trichoptera		27	10	19	10
Simuliidae		13	79	6	33
Chironomidae		9	1	13	28
Ephemeroptera		11	1	15	8
Plecoptera		9	1	6	2
Tipulidae		.	.	1	+
Odonata		2	+	2	+
Hydracarina		+	+	+	+
Ostracoda		.	.	+	+
Amphipoda		1	+	+	+
Gastropoda		3	1	1	1
Miscellaneous (aquatic)		2	+	1	+
Coleoptera		6	1	3	1
Homoptera and Hemiptera		2	+	+	+
Aphidae		.	.	1	+
Formicoidea and Apoidea		8	5	4	2
Isoptera		1	+	.	.
Miscellaneous (terrestrial)		5	+	4	1
Fish		1	+	21	13
Fish eggs		+	+	.	.

examined were collected as monthly samples from the Birket, a small stream which is described below. In addition, specimens of *G. aculeatus* were obtained from two other localities. A large sample of over 500 fish was collected near Troutbeck on the eastern shore of Windermere, Westmorland, on 19 November 1947, by the laboratory staff of the Freshwater Biological Association, and of these, 120 specimens were examined for stomach contents. On 20 August 1946, Dr H. D. Slack collected 28 *G. aculeatus* in a flooded quarry on Easdale Island, Argyllshire, and he kindly allowed us to study them. On 12 June 1948, at our request, he collected a further 27 fish. The stomach contents of all 55 have been examined.

Windermere is a large, deep, mesotrophic, soft-water lake with stony shores, the fauna of which has been extensively studied: see Frost (1946*a*) for literature.

Easdale Quarry is, Dr Slack informs me, near the sea and brackish (3550 mg./l. of chloride), with a rocky bottom and a maximum depth of 35 m. It is not connected with the sea but must receive spray at times. The *G. aculeatus* in this pool grow to a large size.

The Birket is a small stream which drains the tip of the Wirral Peninsula, Cheshire. It rises on fairly flat land and flows through market-garden, pasture and suburb, finally entering the River Mersey not far from its mouth. It is slow flowing and extremely muddy and tends to stagnate in summer, when long reaches of it become choked with *Sparganium erectum*, *Butomus umbellatus* or *Phragmites communis*. In stagnant reaches masses of *Lemna minor* and *Spirogyra* sp. develop, and clumps of *Callitriche* sp., *Elodea canadensis* and *Potamogeton* sp. are common. Much domestic rubbish is thrown into the stream and there is some farmyard and sewage pollution. For most of its length it is about 3 yards wide and canalized, and the depth varies from a few inches in dry weather to several feet during floods. There are three similar tributaries. The stream is about 7 miles long, and about 4 miles from its mouth it flows for a short distance within 400 yards of the sea. From that point onwards the water is slightly brackish. The salinity varies with the level, and chloride values up to 3588 mg./l. have been obtained. The oxygen content is normally fairly high, but during stagnation values as low as 4·7 % saturation have been obtained. The water is hard, about 120–180 mg./l. calcium carbonate equivalent. The temperature varies considerably; values as high as 18° C. have been recorded, but it is probable that much higher temperatures occur. The stream does not normally freeze to any depth in winter as it tends to have a strong flow then. On 12 November 1947, during a medium flood, the surface flow was about 25 m./min., and during the summer there is often no visible current. In a few short reaches the stream is heavily shaded by willow or hawthorn and in these reaches there is no aquatic vegetation and a reduced fauna.

The fauna is rich and abundant, and does not vary greatly from end to end of the stream. In the brackish reaches, however, certain salt-water species occur that are absent higher upstream. Most notable amongst these are *Palaemonetes varians* (Leach), *Gammarus zaddachi* Sext. and *Corixa stagnalis* Leach. The distribution of *Hydrobia jenkinsi* Smith is also peculiar, for although it extends beyond the brackish area it has not penetrated the higher reaches of either the Birket or its tributaries.

In an effort to discover the density of the fauna two bottom samples were taken in a fresh-water reach during July and August 1947. The samples were taken with a hand-operated grab which removed the bottom mud to a depth of about 5 cm. over an area 25 × 25 cm. The mud was then screened and the organisms picked out and counted. Very small organisms which were retained, with a considerable amount of mud, on a sieve of fine bolting silk (56 meshes/cm.) were shaken up with 10 l. of water and counted by withdrawing 10 fractions of 1 cc. with a wide-mouthed pipette, the number in the 10 fractions being then multiplied by 1000 to obtain an approximation of the total number in the sample. Table 5 is a list of the most important constituents of the fauna of the stream, as shown by a year's collecting, together with the number per square metre of stream bed as revealed by the samples. It is not claimed that the numerical results are accurate, but it is felt that they demonstrate the great richness of the fauna. The difficulties of the numerical technique were too great to make regular sampling possible. The population of copepods and cladocerans shown by the samples is relatively low when compared with the ostracods, this is presumably because these small and delicate organisms, which were, in fact, far more abundant than ostracods, were broken up and lost during sieving. The small crustacea live among the weeds and débris on the bootom and so cannot be counted from samples taken with a plankton net. Similarly, small *Asellus* and chironomid larvae were certainly broken up or lost.

It is for these reasons, and because of the serious criticisms put forward by Mottley, Rainer & Rainwater (1939) and Leonard (1939) of the relatively simple and satisfactory technique of sampling stony substrata (see p. 37), that bottom samples were discontinued after only two samples had been taken.

Four species of fish have been found in the Birket of which one appears to be rare.

Gasterosteus aculeatus L. and *Pygosteus pungitius* (L.) are abundant, the former being present in greater numbers. Between them these two species occupy the stream-bed to the extent of about 10 specimens per square metre. This density is considerably raised

Table 5. *The macroscopic fauna of the Birket*

Organism	Approximate (no./sq.m.)	Notes
PROTOZOA	.	Not estimated
COELENTERATA		
Hydra vulgaris Pall.	.	Rare
PLATYHELMINTHES		
Tricladida	.	*Dendrocoelum lacteum* Oersted and *Polycelis nigra* Ehr. occasional
Rhabdocoelida	.	Not estimated
NEMATODA	1200*	
POLYZOA	.	*Lophopus* and *Plumatella* present on submerged rubbish, statoblasts very abundant in mud (107, 500 per sq.m.), but many of these empty
ROTIFERA	.	Not estimated
OLIGOCHAETA	39,700	Mostly Tubificidae; egg-capsules 4000 per sq.m.; these worms are even more abundant in the estuary
HIRUDINEA	80†	*Glossisiphonia heteroclita* (L.) and *Herpobdella atomaria* (Carena) frequent; *Haemopsis sanguisuga* (L.) very rare
CRUSTACEA		
Cladocera	60,400*	Mainly *Chydorus sphaericus* (Müll.) *s.s.* with a few *Eurycercus lamellatus* (Müll.); other species infrequent
Copepoda	1,600*	Mostly *Cyclops* spp. and a few *Canthocamptus*
Ostracoda	309,500	Several genera (indet.) present
Asellus aquaticus (L.) *s.s.*	2,079*	
Palaemonetes varians (Leach) / *Gammarus zaddachi* (Sext.)	.	Only in brackish reaches
HYDRACARINA	.	Very rare
ODONATA	.	Nymphs rare: *Ischnura elegans* (Van der Lind.) and *Enallagma cyathigerum* (Charp.) seen on wing
EPHEMEROPTERA		
Cloëon dipterum (L.)	.	Rare
NEUROPTERA		
Sialis lutaria (L.)	16†	Adults on wing in May
HEMIPTERA HETEROPTERA		
Corixidae	.	Common; *Corixa striata* L. common everywhere; *C. sahlbergi* Fieb. frequent; *C. stagnalis* Leach, in brackish reaches, other spp. occasional
Notonecta glauca L.	.	Rare
TRICHOPTERA	.	Frequent; *Limnophilus* 3 spp. indet. frequent
COLEOPTERA		
Haliplus	16	Very frequent; larvae and adults
Dytiscidae	.	Larvae and adults of several spp. occasional
Hydrophilidae	8	Small spp. frequent in vegetation
DIPTERA		
Chironomidae & Ceratopogonidae	4,230*	Larvae and pupae of former abundant, mostly Chironominae; Ceratopogonidae occasional.
Other Diptera	.	Larvae of several families occasional, Dolichopodidae, Tipulidae (s.l.) Culicidae, Psychodidae, Tabanidae, Simuliidae, Anthomyidae and probably others
MOLLUSCA		
Sphaerium lacustre (Müller)	6,780	Abundant in most reaches
Pisidium sp.	.	Very rare
Hydrobia jenkinsi Smith	.	Abundant but absent from higher reaches where numerical samples were taken
Valvata piscinalis (Müller)	.	Very rare
Bithynia tentaculata (L.)	.	Very rare
Planorbis vortex (L.)	24†	Rare, but three present in one sample
Aplecta hypnorum (L.)	.	Rare, absent from brackish reaches
Physa fontinalis (L.)	.	Frequent in certain places, absent elsewhere
Limnaea pereger (Müller)	2,740	Abundant everywhere
Limnaea palustris (Müller)	.	Very rare, a few seen at one point
FISH		
Gasterosteus aculeatus L.	.	See text
Pygosteus pungitius (L.)	.	
Rutilus rutilus (L.)	.	
Gobius minutus L.	.	

* Almost certainly underestimated by samples due to loss and destruction in sorting.
† Almost certainly overestimated by samples.

during the breeding season in areas where spawning occurs. It is roughly estimated that the total population of the Birket and its tributaries is of the order of half a million fish.

Rutilus rutilus (L.) occurs in certain reaches, both fresh and brackish, and shoals of these fish range up and down the stream and its tributaries when the water is sufficiently deep. The total population is probably only a few thousands, and it is probable that this species has been introduced to the stream by overflow from artificially stocked fishponds.

Gobius minutus L. is a species characteristic of estuarine mud flats. On 28 October 1947 five small specimens were caught in one net draught in the uppermost brackish reach. No other specimens have been seen, although the stream has been extensively netted at all seasons. It seems, therefore, either that the species is rare there, or that these five fish were a chance introduction. They were too far upstream to have been brought by the tide.

2. *Stickleback forms examined*

The *Pygosteus pungitius* belonged to the forms *hologymna* and *carinata* as defined by Bertin (1925); as stated by him only the largest specimens possessed a caudal heel.

The *Gasterosteus aculeatus* from the Birket all belonged to the race *gymnura* as defined by Bertin, or the type A^m as defined by Heuts (1947). Those from Windermere were largely *gymnura* with a few (5%) *semiarmata* and were therefore types A^m and A^i of Heuts. The Easdale fish were all *trachura* and so belonged to the type B^m of Heuts. The material investigated belongs therefore to the two distinct races *A* and *B*.

3. *Methods and technique*

All fish from the Birket were caught with a small seine net made of mosquito netting, or with two similar shorter nets which were placed across the stream and brought together before being lifted. The Windermere sample was collected with a seine net and the Easdale fish were caught with rod and line. The fish were preserved in the field, in formalin or alcohol, soon after capture, and examination was usually made within 2 or 3 weeks.

All fish were measured from the snout to the tip of the middle fin-ray of the tail, and the length was recorded to the nearest millimetre below.

Each stomach was dissected out of the fish and opened under a low-power binocular microscope. The contents were picked out on to a microscope slide, flooded with fluid and examined; when necessary a high-powered microscope was used also. Each food species was identified as far as possible, and allotted points as described above. At the same time, notes were made of the maximum and minimum numbers of each food species present in the sample and, where species were assessed together, of their relative abundance.

4. *The food of* Gasterosteus aculeatus

(*a*) *Review of the literature*

Several early authors give lists of the food of the three-spined stickleback (Lacépède, 1802; Day, 1880–4; Smitt, 1892; Tate Regan, 1911), and similar lists occur in more recent papers (Bertin, 1925; Leiner, 1930; Heilborn, 1931; Fisher, 1948). These authors agree that the diet consists of worms of various kinds, small Crustacea, aquatic insects and larvae, drowned aerial insects and the eggs and fry of fish including their own. Leiner adds infusoria as part of the diet of young fish. Several authors comment on Stickleback's voracity; Day states that they have been observed to kill and eat larger fish in aquaria, and Bertin says that they are regarded as pests in fish hatcheries, etc. Their voracity is well known to the children who catch them with a worm tied to a piece of string without a hook. Leiner states that they can be caught in this manner only during the breeding season and that it is only females which are so caught, as the males feed little at this time.

Only three workers have made any detailed study of the food of this species.

Saunders (1914) examined 'a great number' of sticklebacks from a pond near Cambridge, and found that at all times of the year the stomachs of large fish were full of the diatom *Nitzschia sigmoidea* Ehbr., but that the smaller fish in the pond tended to be carnivorous, and ate insect larvae and small Crustacea. In nearby ponds all the fish were carnivorous, and those from the first became so in aquaria. He discusses the feeding habits of the fish and concludes that they hunt by sight and are selective. He suggests that local conditions affect feeding preferences.

Blegvad (1917) investigated the stomach contents of 736 specimens caught in the *Zostera* region of various Danish waters. All of these are brackish waters, and it seems probable that all his specimens, some of which were large, belonged to race *B*. He states that the young fish feed on copepods (Calanoida and Harpactoida), cladocerans, mollusc larvae and ostracods, and that as they grow they begin to eat the young of gammarid amphipods, the isopod *Idotea* and mysids, the isopod *Jaera*, the amphipod *Corophium*, insect larvae and winged insects from the water surface. Specimens were also found with their stomachs distended with conifer (? fir) pollen, and they also ate the eggs of other species of fish and of other sticklebacks. His results, which for 427 fish are assessed by the weight method and tabulated, show

that Crustacea form most of the food, and that insects and fish eggs and fry are the next two most important items. These results have been recalculated from his table to show percentage composition of the diet for comparison with the results of the present investigation (Table 6).

Table 6. *The percentage composition of the food of* 427 Gasterosteus aculeatus *and* 112 Pygosteus pungitius *from Danish brackish waters. Data assessed by weight method and recalculated from Blegvad* (1917)

Food item	Composition of food (%)	
	G. aculeatus	*P. pungitius*
Pelagic lamellibranch larvae	+	.
Gastropoda, eggs and larvae	1	.
Polychaeta	1	.
Higher Crustacea	41	28
Copepoda	27	38
Ostracoda	1	5
Cladocera	10	.
Winged insects	4	.
Insect larvae	4	2
Ophioglypha albida	+	.
Appendicularia	+	.
Actinia viduata	1	.
Fish eggs and larvae	8	28
Pollen of conifers	+	.
Algal threads	1	.
Size range (cm.)	0·2*–11	2–5

* *Sic*, but this species is 0·5 cm. long when it hatches in the Birket.

Hartley (1940) examined the stomachs of 129 fish from two Cambridgeshire rivers. These fish probably belonged to race *A*. His results, which are assessed by the occurrence method, show that insects formed 60% of the food and Crustacea 29%. A few small molluscs and some plants and diatoms were also eaten. Of the insects 80% were aquatic fly larvae and 16% mayfly nymphs; 80% of the Crustacea were copepods, and other planktonic forms, *Chydorus* and ostracods making up another 18%. Crustacea were the most important food in winter. In the other 9 months of the year insects predominated. He found no evidence of a winter fast. Similar findings resulted from a reconsideration of part of these data together with some other fish (Hartley, 1948); 227 fish were examined from the River Cam, and it was found that the food, assessed by the occurrence method, consisted of molluscs 2%, insects 51%, arachnids 1%, Crustacea 24%, oligochaetes 1%, vascular plants and filamentous algae 14%, and diatoms 8%. Most of the insects were chironomid larvae and pupae, but mayfly nymphs were fairly important. Most of the Crustacea were copepods, but *Chydorus* sp. and to a lesser extent ostracods were also important. *Asellus* and *Gammarus* were unimportant.

(*b*) *Food species found in the present investigation.*

Gasterosteus aculeatus swallows its food without chewing it, and in most instances it is fairly easy to identify the organisms present in the stomach.

The percentage composition of the food, and the number of specimens examined from the three localities, are shown in Table 7. Comment has already been made on the great similarity in result obtained by three separate methods of assessment. In order, however, to avoid any confusion, all figures quoted below refer to the points method.

Arcella occurred in small numbers in April and July in fish from the Birket.

Rotifera of various genera occurred during the summer and autumn in fish from the Birket, with a few occurrences in February. *Euchlanis*, *Salpina*, *Philodina* and *Noteus* were tentatively identified, the last being particularly abundant in October. Usually only one or two specimens occurred in each fish but 115 were found in a 22 mm. fish in October.

Nematoda, other than parasites which are dealt with below, were infrequent, occurring in only seven fish from the Birket.

Invertebrate eggs and statoblasts: unidentified invertebrate eggs occurred occasionally particularly in small fish. A few fish had eaten statoblasts of *Lophopus* and *Plumatella* in the Birket.

Aquatic Oligochaeta formed an important part of the food of the larger fish in the Birket and in Windermere. Those from the Birket were probably tubificids. Six specimens were found in a 41 mm. fish, but counts were usually impossible. The egg packets of these worms were often eaten, as many as 49 being found in a 48 mm. fish.

Other Annelida: three large fish from the Birket contained large earthworms, and two contained leeches (*Glossiphonia* and *Herpobdella*). An unidentified leech was present in a fish from Easdale.

Sphaerium lacustre occurred frequently in stomachs in the Birket during the winter but rarely in the summer. Specimens eaten ranged from 0·9 to 1·5 mm. across, and usually few were present, although 14 were found in one fish. A very few specimens of *Pisidium* sp. were found in October, one being 2·4 mm. across. These have been included with *Sphaerium* in the tables.

Hydrobia jenkinsi was equally important in the Birket, and similarly occurred chiefly in the winter. It is possible that it is also eaten in the summer, but most of the summer samples were taken above the range of this species in the Birket. Normally a few specimens occurred in each fish, but 232 were found in a 56 mm. fish. Specimens up to 2·1 mm. high were eaten.

Other Mollusca occurred occasionally in the Birket fish. The species found were *Valvata piscinalis* (one

Table 7. *The percentage composition of the food of* Gasterosteus aculeatus *in the three localities studied and the change in composition of the food with increase in size of the fish*

	The Birket, Cheshire												Easdale Quarry, Argyll		
	Size groups						Total			Windermere					
No. of fish ...	137	429	444	373	162	36	1581			120			55		
Size range (mm.) ...	6–	20–	30–	40–	50–	60–73	6–73			21–53			38–96		
Method of assessment ...	P	P	P	P	P	P	P	O	D	P	O	D	P	O	D
Arcella	+	+	.	.	.	.	+	+	.	.	.	.	.	.	.
Rotifera	2	2	+	+	.	.	1	2	+	.	.	.	.	.	.
Nematoda	.	+	+	+	.	.	+	+	.	.	.	.	.	.	.
Invertebrate eggs etc.	2	+	+	+	+	.	+	1	+	+	+	.	.	.	.
Aquatic Oligochaeta	.	7	14	10	13	15	10	6	11	6	4	8	.	.	.
Other Annelida	.	.	+	.	1	.	+	+	+	.	.	.	1	1	2
**Sphaerium lacustre*	.	1	5	4	2	4	3	2	3	.	.	.	.	.	.
Hydrobia jenkinsi	+	4	3	2	1	1	3	2	3	.	.	.	.	.	.
Other Mollusca	.	+	+	1	+	.	+	+	+	.	.	.	.	.	.
Hydracarina	+	.	.	.	.	.	+	+	.	.	.	.	.	.	.
Cladocera	41	10	6	9	3	7	11	12	11	32	36	27	.	.	.
Copepoda	28	28	17	14	10	8	19	20	20	40	30	44	5	4	6
Ostracoda	2	6	3	3	2	2	4	7	2	7	13	5	.	.	.
Higher Crustacea	1	6	9	16	24	17	11	7	12	3	2	5	73	56	70
Ephemeropteran nymphs	.	+	1	+	+	.	+	+	+	1	1	.	.	.	.
Aquatic Hemipteran nymphs	.	.	+	1	1	.	+	+	+	.	.	.	.	.	.
Trichopteran larvae	.	.	1	2	2	7	1	1	1	2	1	2	.	.	.
Aquatic Coleopteran larvae	.	1	+	+	+	+	+	+	+	.	.	.	.	.	.
Chironomid larvae (etc.)	20	17	18	15	17	6	17	15	17	8	10	8	.	.	.
Chironomid pupae	.	2	4	8	6	7	4	3	5	.	.	.	3	6	2
Other Dipteran larvae	.	2	2	4	3	2	2	2	2	.	.	.	4	6	6
Unidentified Arthropoda	+	+	1	1	1	+	1	1	+	+	+	.	.	.	.
Stickleback eggs (and larvae)	.	+	.	1	3	16	1	1	1	.	.	.	2	4	2
Spiders	.	.	.	+	.	.	+	+	.	1	+	1	.	.	.
Collembola	.	+	1	1	.	.	1	1	1	+	1	.	.	.	.
Homoptera	.	1	1	1	.	.	1	1	1	.	.	.	1	1	2
Thysanoptera	.	+	+	+	.	.	+	+	+	+	+	.	.	.	.
Hymenoptera	.	.	+	.	.	.	+	+	.	.	.	.	.	.	.
Dipteran adults	+	+	1	+	+	.	+	+	+	.	.	.	4	7	4
Ephemeropteran adults	.	.	.	.	+	.	+	+	+	.	.	.	.	.	.
Lepidopteran larvae	.	+	+	1	2	.	1	+	1	.	.	.	.	.	.
Diatoms	1	5	5	1	+	.	3	2	3	.	.	.	.	.	.
Closterium	+	2	+	+	.	.	1	1	+	.	.	.	.	.	.
Filamentous Algae	+	+	+	+	+	.	+	1	+	.	.	.	3	3	4
Other Algae	2	+	.	.	.	.	+	1	+	.	.	.	.	.	.
Higher plant tissue	+	1	2	3	4	7	2	3	2	+	+	.	2	6	2
Mineral matter	+	+	+	+	+	1	+	1	.	.	.	.	1	4	.
Detritus, unidentified, etc.	.	3	4	2	2	+	3	3	2	.	.	.	1	1	.
Percentage of fish with empty stomachs	2·9	4·0	5·4	6·4	8·0	8·3		5·3			6·7			10·9	

P = points method; O = occurrence method; D = dominance method.

* Includes a few *Pisidium* too.

specimen 1·9 mm. high), *Physa fontinalis* (three specimens, one 4 mm. high), *Aplecta hypnorum* (two specimens, one 2·4 mm. high), and *Limnaea pereger* which occurred in seven fish in June and July, fourteen being present in one fish; probably at other times of the year this species was too large to be eaten.

Hydracarina occurred once only, in a fish from the Birket. This may have been due to their rarity there (Table 5), or to the fact that many species are distasteful to sticklebacks, as has been shown by Elton (1922), who suggests that the bright scarlet colour of so many species is probably an example of Müllerian mimicry.

Cladocera in the Birket consisted almost entirely of

Chydorus sphaericus, but a few *Eurycercus lamellatus* were eaten during the summer as were a very few specimens of *Simocephalus* sp. The last species was never found alive in the stream and so was presumably rare. Enormous numbers of *Chydorus* were often present, as many as 1921 being counted in a 43 mm. fish in May; 400–500 were found frequently. In Windermere the commonest cladoceran in the stomachs was *Bosmina*, but also present were *Eurycercus*, *Alanopsis*, *Chydorus*, *Alona*, *Daphnia* and *Leptodora*, which last only occurred in the larger fish. This list indicates that the Windermere fish were feeding both in the littoral zone and in the open water. Copepoda in the Birket consisted largely of *Cyclops* spp., but a few specimens of *Canthocamptus* were eaten. Large numbers were often present, but they were usually crushed and broken and impossible to count. Several hundred were counted on occasions and about 100 frequently. Nauplii and other young stages occurred throughout the year. In Windermere both *Cyclops* and *Diaptomus* had been eaten, the latter being less common. In Easdale copepods only occurred in the smaller fish; the genera were not determined.

Ostracoda occurred fairly frequently in fish from the Birket and Windermere; several undetermined genera were present. The numbers eaten were usually below 10, but up to 47 adults were found occasionally, and larger numbers of young specimens were found in a few fish in September.

Higher Crustacea in the Birket consisted almost exclusively of *Asellus aquaticus*, but four specimens of *Gammarus zaddachi* and one small *Palaemonetes varians* were found in large fish from the brackish reaches. The largest *Gammarus* was 10 mm. long. *Asellus* of all sizes were eaten at all seasons, although, unaccountably, none was found in March. In general, the largest specimens occurred in the largest fish, but large fish often contained small specimens. Several fish were found which contained only an odd leg or other appendage. This presumably resulted from the fish's habit, often observed in aquaria, of repeatedly spitting out and re-catching prey before it is finally swallowed, which often results in detachment of appendages and the escape, or seizure by another fish, of the prey. Some large fish contained two or three full grown specimens, and as many as 36 specimens of various sizes were found in a single fish. In Windermere, *Asellus* was the only higher crustacean found in the stomachs. In Easdale, the principal crustacean in the stomachs was *Gammarus duebeni* Lilljeb., but a few specimens of *Orchestia gammarella* (Pallas) had also been eaten. Specimens of all sizes had been eaten, and the large fish often contained several large specimens. In four Easdale fish parts of *Ligia oceanica* (L.) were found.

Ephemeropteran (mayfly) nymphs occurred occasionally throughout the year in the Birket fish. The species was almost certainly *Cloëon dipterum*. The nymphs were all small and usually occurred singly. In the Windermere fish one small baetid and one small ecdyonurid were found.

Aquatic Hemiptera: nymphs of *Corixa* were found in only 17 fish from the Birket during May to July. The commonest species in the stream was *Corixa striata*. All the specimens were below 2·0 mm. in length, and usually one to five specimens were present, but one fish had eaten 25.

Trichopteran (caddis) larvae in the Birket consisted entirely of *Limnophilus* spp., but in the Windermere fish several genera were present. Although they occurred in several months of the year they were most abundant in the spring (Table 8). Large specimens up to 18 mm. long had sometimes been eaten and usually only one larva was present. In only one stomach from the Birket was the larval case also present, but in Windermere one fish 52 mm. long had eaten eight leptocerid larvae in their cases. Perhaps the compactness of leptocerid cases compared with the unwieldy cases of *Limnophilus* accounts for this.

Beetle larvae were found only in fish from the Birket and their occurrence was sporadic. Usually they occurred singly and all were less than 10 mm. long. Most were dytiscids, but a very few hydrophilids and one *Gyrinus* were found.

Chironomid fly larvae and pupae were abundant in all samples from the Birket, the larvae being common at all seasons but the pupae commonest in the spring (Table 8). In the Windermere fish many larvae occurred and a few pupae were found in the Easdale fish. Ceratopogonid larvae, which were scarce, and probably ceratopogonid pupae also, have been included in this category. No endeavour was made to identify these larvae, which were mostly 'bloodworms'. Larvae and pupae of all sizes were eaten, as many as 40 larvae or six pupae occurring in a single stomach.

Other fly larvae consisted mainly of small dolichopodid or empid larvae of which up to 30 were sometimes present, and of unidentified cyclorrhaphan maggots, particularly in winter. In addition, a few tipulid and psychodid larvae were found, and one fish from Easdale quarry had eaten a *Chaoborus* larva.

Stickleback eggs were found frequently during the breeding season and they were eaten primarily by the large fish. Only one fish, a 44 mm. female, had eaten a larva, itself 7 mm. long and so free of the nest. Up to 40 eggs occurred in a stomach, and were in all stages of development, from entirely undeveloped to the point of hatching. Of 22 fish from the Birket which had eaten eggs 17 were males, of which only three were not in breeding colour, and five were females which were either ripe or partly spent. The eggs in one of the females were partially developed and so pre-

Table 8. *The percentage composition of the food of* Gasterosteus aculeatus *in the Birket month by month. Percentages are assessed by the points method, and only those food items forming at least 5 % of the food in any one month are included. The various food items are arranged as far as possible in the order of their successive maxima*

Food item	Month of capture											
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Cladocera	33·4	39·2	3·5	1·6	9·2	0·8	0·2	0·7	5·3	11·3	6·0	20·5
Copepoda	10·5	27·9	38·2	11·9	25·0	6·5	15·0	11·6	20·1	27·8	23·4	14·0
Ostracoda	2·4	0·8	10·5	6·7	4·1	4·2	5·0	0·6	0·6	3·5	0·9	3·4
Algae	7·6	2·9	9·4	22·4	6·2	0·8	0·1	0·1	0·1	0·1	.	0·7
Asellus	7·8	6·7	11·4	19·6	12·7	15·2	19·0	7·4	6·2	.	13·0	6·3
Higher plant tissue	0·4	0·3	.	0·4	2·0	9·9	1·7	2·4	3·8	1·2	1·9	2·1
Terrest. Arthropoda	0·1	+	.	3·7	1·8	9·7	5·7	1·6	0·2	1·7	2·0	4·4
Mollusca	3·0	0·9	0·3	2·3	9·1	23·8	12·3	15·7	2·3	1·3	0·8	0·7
Detritus, etc.	.	.	.	3·8	4·2	5·7	3·2	13·1	1·8	.	0·6	1·1
Other Dipteran larvae	.	1·5	.	2·0	0·7	0·3	3·7	9·7	2·4	1·2	0·3	5·8
Oligochaeta	+	.	.	1·0	5·1	2·5	16·9	13·3	39·6	3·9	1·2	0·9
Trichopteran larvae	0·9	.	.	0·2	.	.	.	0·7	1·5	14·2	1·8	.
Chironomid pupae	2·5	1·3	1·9	0·5	3·7	0·3	0·5	0·6	0·7	14·5	18·5	15·7
Fish eggs and larvae	1·7	.	.	.	.	.	.	.	.	.	8·1	3·5
Chironomid larvae	23·7	15·6	23·4	21·8	8·7	18·7	15·9	18·8	11·5	17·1	20·0	14·5

sumably came from a nest. It seems therefore that not only do males eat eggs from their own nests, as often occurs in aquaria, but that non-breeding males and females also raid the nests for eggs. It is possible also that ripe females occasionally shed eggs away from nests, but these would presumably never start to develop. Most of the eggs eaten appeared to be those of *Gasterosteus aculeatus*, but one female contained three eyed eggs of *Pygosteus pungitius*, whose eggs are smaller (Leiner, 1934). In view of the speed with which larvae are eaten in aquaria, and of the great numbers present in the breeding sites, it is surprising that out of 327 fish examined from the Birket during April, May and June only one should have eaten a larva.

Spiders: one was found in a Birket fish and one in the Windermere sample.

Collembola occurred in only one fish from Windermere, but were not infrequent during the winter in the Birket, where 30 fish were found to have eaten them. Several species were eaten, and as many as 141 individuals occurred in one fish. Often these insects occurred together with small Homoptera, and so were presumably drowned or drowning.

Hemiptera Homoptera of the families Aphididae, Psyllidae and Jassidae occurred in 29 fish from the Birket between September and December, with one occurrence in May. Aphidae were the most frequent and were usually winged forms, but several nymphs were found in December when as many as 13 were present in one fish. One psyllid was eaten and several jassids, of which two were nymphs. An adult jassid was eaten by a fish from Easdale. These insects were presumably in the water when eaten.

Thysanoptera: five fish from the Birket and one from Windermere had each eaten a thrips, of which four were nymphs.

Hymenoptera: one parasitic species, a chalcidoid adult, was found in a fish from the Birket.

Adult flies were found in fish from the Birket and Easdale. They were eaten at all seasons and were mostly chironomids, but one anthomyiid and one syrphid were found.

Ephemeropteran (mayfly) adults: only one mayfly was found, in a fish caught in the Birket during April. It was probably *Cloëon dipterum*.

Lepidopteran larvae occurred in various months, and in May made 4 % of the food of the fish from the Birket. Several types of caterpillar were eaten, and they usually occurred singly. Specimens up to 11 mm. long were found.

Algae apparently normally form a small proportion of the food, and they appear to be eaten by accident at most seasons. Types found in the Birket included *Spirogyra*, *Closterium*, *Eudorina*, *Microcystis* and the diatoms *Synedra*, *Surirella*, *Pleurosigma*, *Gomphonema*, *Fragilaria* and *Navicula*. Generally speaking, each monthly sample had a characteristic alga; for instance *Eudorina* was found only in July, and *Closterium* was particularly frequent (8 %) in August. Diatoms, however, showed a maximum (22 %) in September and were still common (6 %) in October. During August *Closterium* was often a dominant foodstuff, and during September diatoms were frequently dominant and this continued into October. This is discussed more fully below.

Higher plant tissue of various types, including bark, grass, *Potamogeton*, seeds, etc. occurred in all three

localities. Mineral matter, consisting of sand and small stones, was not infrequent. Detritus, which closely resembled higher plant tissue which was too finely divided to show structure, was often found, and included with it in the tables are certain unidentified structureless substances that were found in some stomachs. Included in this category also are several pieces of hair, two small feathers and a piece of silver paper.

(*c*) *Food eaten in the three localities*

Table 7 shows that whereas there is little difference between the composition of the food of *Gasterosteus aculeatus* in the Birket and in Windermere, apart from the generic and specific differences mentioned above, the food of the fish from Easdale is greatly different. This is surprising because not only are the Birket and Windermere very different types of water, but both Easdale Quarry and much of the Birket are brackish. It seems possible therefore, that the difference between the diets of these localities depends, not on local conditions, but on the fish themselves. It has already been pointed out that the Easdale fish belong to race *B*, and it is possible that the difference in feeding habit is another racial difference to be added to those listed by Heuts.

Admittedly, only a few fish from Easdale were studied, and many of these are abnormally large (Table 7), and, as is shown below, large fish tend to eat more large Crustacea, but even many medium-sized fish from Easdale were full of *Gammarus*. It seems improbable that smaller Crustacea were very scarce in a quarry pool, and chironomid fly larvae were certainly present.

The work of Blegvad and Hartley supports the thesis that these two races elsewhere show the same differences of diet. Table 6 shows that Blegvad found that his fish, which were presumably race *B*, ate more higher Crustacea than anything else, and that aquatic insects were unimportant. Hartley, on the other hand, working presumably on race *A*, gives figures, quoted above, showing that, as in the Birket and Windermere, copepods, cladocerans and insects were the chief items in the diet. It seems, therefore, that on the whole race *A* feeds largely on entomostraca and insects, while race *B* concentrates more on higher Crustacea. It is, however, possible that this is merely a reflexion of the generally greater size of race *B*, and the fact that they live in brackish or salt water where higher Crustacea are abundant.

(*d*) *Food eaten by fish of different sizes*

Table 7 shows the percentage composition of the diet of various size groups of race *A* fish from the Birket. The small fish feed largely on copepods, cladocerans and chironomid larvae, and as they grow their diet becomes more varied, and other forms such as oligochaetes, molluscs, higher crustacea (*Asellus*), chironomid fly pupae and algae become important. Certain forms, such as cladocerans and copepods, decrease in importance as the fish grow; while others, such as higher Crustacea, caddis larvae and chironomid pupae, increase in importance. The diet of fish over 60 mm. long will be seen roughly to resemble the diet of race *B* fish from Easdale Quarry and from Danish brackish water (Table 6), but 40% of the Easdale fish were below 60 mm. long and Blegvad's fish were of all sizes; it is to be noted, however, that the minimum size given for the latter is questionable.

The change in composition of diet as the fish grow is an expression of increase in the maximum size of the organisms eaten. Small fish are unable to swallow relatively large organisms like molluscs and chironomid pupae, and as they grow it becomes less worthwhile to catch small organisms. Allen (1935) has shown that perch would need to eat enormous numbers of small Crustacea if they did not change their diet as they grow. Nevertheless, unlike perch, which grow to a large size, 3-spined stickleback, of race *A* at least, never grow too large to fail to eat at least some of the animals of a size that can be eaten by the smallest fish.

It will be noted that as the fish grow the percentage with empty stomachs increases steadily. This presumably indicates that the fish eat more sporadically as they grow larger.

(*e*) *Seasonal variation*

Table 8 shows that the composition of the food varies throughout the year, and that each important food item tends to have a maximum importance at a certain season. The only exception to this appears to be chironomid larvae, which are about equally important in all months. This is probably because many species are here assessed together, each individual species would probably show its own maximum.

The seasonal fluctuations are probably due partly to actual variation in numbers of the various food items in the habitat (e.g. *Chydorus sphaericus* the most important cladoceran in the Birket is relatively rare there in winter), and partly to varying relative availability. During the winter cladocerans and copepods are scarcer than in summer, and the fish are driven to eat such things as molluscs and oligochaetes, which, although always present, appear to be less attractive, or are perhaps not as easy to eat or find as small Crustacea.

Seasonal occurrence of maxima of such organisms as fish eggs and larvae and chironomid pupae is to be expected, and it is probable that size at a given season is a controlling factor for others such as caddis larvae

which may be too large to be eaten at certain seasons.

It seems probable also that in other bodies of water, where conditions and the specific composition of the food items are different, the time of the seasonal maxima would be different. For instance, in Windermere in November cladocerans were important (32 % of food), whereas in the Birket they formed only 1 % in this month. Similarly, Hartley (1940) found that Crustacea were the most important food in winter, whereas in the Birket they were not.

Two interesting winter maxima are higher plant tissue and terrestrial arthropods. The former is available at all times and is presumably eaten mainly in winter because of food scarcity, but the latter are apparently least available in winter. Possibly winter scarcity, combined with winter floods, which must wash many terrestrial organisms into the water, account for this.

The seasonal occurrence of algae needs special comment. During the spring algae were unimportant, in summer and early autumn they formed up to 9 % of the diet, but in September and October their importance increased greatly, diatoms being the principal algae eaten. The totals shown in Table 8 for September and October are, however, misleading, as these are based on all the fish taken during these months, whereas the habit of eating large quantities of diatoms was shown only by fish from large shoals which formed at this season. Diatoms were found to constitute 49 % of the food of 63 fish from a large shoal in September, while 29 fish taken in the reaches above the shoal, and 45 from reaches below the shoal had eaten no algae at all. Similarly, in early October, when shoals still occurred, 40 fish from shoals had eaten diatoms in large amounts (25 %), whereas 112 other fish some of which were taken in the locality occupied in September by a large shoal, had eaten very few algae (< 1 %). It seems therefore that only fish in large shoals eat large amounts of diatoms.

It seems possible that this phenomenon is connected with the crowding that occurs during shoaling, which may result in scarcity of immediately available animal food. This suggestion is perhaps supported by the work of Saunders (1914), quoted above. He recounts that he caught fish by using a worm over a net as a lure, and that a great number of fish came to the worm. This indicates that the fish were plentiful in the pond and that they were hungry. It is possible that during the period of his investigation the pond was overcrowded, and that the fish, despite their obvious preference for animal food, were driven to eat diatoms. Saunders comments on the fact that only one species of diatom was eaten, despite the fact that many others must have been available. In the Birket the same phenomenon was often observed, and it was noticeable that the most favoured algae were all, like *Nitzschia*, elongate (e.g. *Closterium*, *Synedra*, *Pleurosigma*, *Surirella*, and *Fragilaria*). Hartley (1948) also found that diatoms were a fairly important food item. It would be interesting to know if he found them only in fish from large shoals.

Table 9 shows the average number of points allotted per fish, and the percentage of fish with empty stomachs in each month. It will be seen from the former that there was a slight decrease in food eaten during the winter, and that during the breeding season, late March to June, feeding was rising to its maximum in July and August. The percentage of empty stomachs, which has often been used as an estimate of feeding activity, does not show this, but there was a marked peak in March, at the beginning of the breeding season. Of the fish with empty stomachs in the March sample 80 % were females, and this is almost identical with the proportion of females in the sample. This indicates that failure to feed at this season is not confined to one sex as Leiner supposes. This is supported by the fact that the number of points gained by males and females in March, April and May were not significantly different at P 0·05.

Table 9. *The amount of food taken month by month by* Gasterosteus aculeatus *in the Birket and percentage of fish with empty stomachs*

Month	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
No. of fish examined	109	112	82	137	152	99	230	100	243	99	88	130
Fish with empty stomachs (%)	0·9	4·5	1·2	1·5	6·6	8·1	5·2	3·0	7·4	15·2	6·8	3·1
Average number of points per fish	17·2	18·5	18·2	16·3	14·4	14·8	14·8	12·3	14·2	13·4	14·6	17·2
Average number of points per fish excluding fishes with empty stomachs	17·4	19·4	18·4	16·5	15·4	16·1	15·7	12·8	15·3	15·8	15·7	17·8

The average numbers of points allotted per fish, excluding those with empty stomachs, show that, in March, fish which were feeding ate more than those feeding in the winter. In other words, feeding merely became more intermittent at the beginning of the breeding season, but once breeding was fully in progress in April and May feeding became more steady and increased.

Hartley (1940), basing his statement on numbers of empty stomachs, states that this species has no winter fast. The data given above, however, show that there is a definite seasonl rhythm in feeding activity. It is

possible that the winter decrease in food intake is connected with locality and availability and not with temperature. In the Windermere sample, however, which was taken in November, the average number of points was 11·0, which is actually lower than the figure for the Birket in this month. It is well known that in other species of fish temperature influences feeding (Scheurung, 1928; Markus, 1932; and others).

5. *The food of* Pygosteus pungitius

(*a*) *Review of the literature*

Only three authors mention the food of the 10-spined stickleback. Forbes (1883) examined the stomachs of two specimens in North America, and found that they contained *Simulium* and *Chironomus* larvae (60%) and *Chydorus* and other cladocerans (40%). Smitt (1892) states that the food consists of worms, insects, fish-roe and bits of grass. Blegvad (1917) investigated the stomach content of 142 specimens from Danish brackish waters. He includes this species in the general remarks made on *Gasterosteus aculeatus* (see p. 43), but his tabulated results for 112 fish, assessed by the weight method, show that he found no vegetable matter in the stomachs and no cladocerans. His data have been recalculated for comparison with the results of the present investigation (Table 6). It will be seen that Crustacea and, strangely, stickleback eggs form most of the food. One can only assume from this that most, if not all, of the 112 specimens were caught during the breeding season.

(*b*) *Food organisms found in the present investigation*

The same general remarks apply to this species as to *G. aculeatus*. Table 10 shows percentage composition of the food of 656 fish from the Birket, and, as for *G. aculeatus*, it will be seen that the points, occurrence and dominance methods give substantially the same result. As before, however, all figures given below refer to the points method.

Rotifera were few and infrequent, occurring in only four fish in August and October; eight specimens were present in one fish. Only *Noteus* was identified but other genera were present.

Nematoda other than parasites occurred only once.

Invertebrate eggs: unidentified eggs were found in three fish.

Aquatic Oligochaeta were a fairly important food item, except during June, July and August: they were probably tubificids. Only one fish had eaten an egg-packet.

Sphaerium lacustre occurred in several months. Up to eight were present per fish and they were of the same general size as those eaten by *Gasterosteus aculeatus*.

Hydrobia jenkinsi was less important, and similarly appeared to be a winter food. It was, however, absent from the upper reaches of the Birket where the spring and summer samples were collected. Up to eight were present per fish and they ranged from 0·5 to 1·4 mm. high.

Other Mollusca consisted of *Limnaea pereger* in June (three occurrences of small specimens), *Planorbis spirorbis* in October (one specimen 2·1 mm. across), *Aplecta hypnorum* in March (two specimens 2·2 and 2·7 mm. high) and one small specimen of *Physa fontinalis* in June.

Hydracarina: two single occurrences in June.

Cladocera were abundantly eaten at all seasons, except the winter (November to February) which was not adequately sampled (see below). Most were *Chydorus sphaericus*, but *Eurycercus lamellatus* was abundant in summer and a few specimens of *Simocephalus* were found during the autumn. Over 500 *Chydorus* were found in a 44 mm. fish, but usually fewer than 100 were present per stomach.

Copepoda were probably all *Cyclops* spp., and were important in all months studied, occurring in three of the eight winter fish examined. Up to 100 were present, and in October large numbers of nauplii and juvenile stages were eaten.

Ostracoda occurred fairly frequently in small numbers in all months adequately sampled.

Higher Crustacea consisted almost entirely of *Asellus aquaticus*, only two small *Gammarus zaddachi* being found in a fish caught in brackish water. *Asellus* of all sizes were eaten, and as many as 27 were found in one fish. As in *Gasterosteus aculeatus* several fish contained only an odd leg or antenna.

Ephemeropteran (mayfly) nymphs, which were presumably *Cloëon dipterum*, occurred in 14 fish in August, September and October. Usually only one specimen was present per fish.

Aquatic Hemiptera: one nymph of *Notonecta*, 2·8 mm. long, was found in a large (48 mm.) fish in May.

Trichopteran (caddis) larvae were found in several fish in the spring and one was eaten in October. All were small *Limnophilus* sp. and were without their cases.

Beetle larvae were found singly and sporadically, all were small, and all but one were Dytiscidae.

Chironomid fly larvae and pupae were abundant in all samples, but the pupae occurred chiefly in the spring. Most of these were 'blood-worms' but some may have been Ceratopogonidae. Up to 30 occurred in one fish.

Other fly larvae consisted mostly of dolichopodid or empid larvae, but a few culicine larvae, tabanid larvae and cyclorrhaphan maggots were also eaten.

Stickleback eggs and larvae were only eaten during the breeding season (April to June). Three larvae had

been eaten, one by a small immature male 18 mm. long and two by adult males in full breeding colour. One of these had eaten a larva only $3\frac{3}{4}$ mm. long which still had its yolk sac; this larva had therefore not left the nest, but it is possible that it had died there and been eaten by the watching male. Eight fish had eaten eggs, all of which were undeveloped. Six of these fish were males with varying amounts of breeding coloration and two were adult females. The eggs in two of these fish, a female and a partly coloured male, appeared to be those of *Gasterosteus aculeatus* (Leiner, 1934). A maximum of seven eggs occurred in one fish. It seems therefore that this species, unlike *G. aculeatus*, does not raid nests and eat developing eggs, but it is possible that further investigation would show that it does so, especially as Blegvad found that eggs were so important a part of the food. It is possible that ripe females of both species shed eggs away from nests, and possibly males eat only eggs from their nests which are failing to develop.

Spiders: one was found in October.

Collembola occurred in two fish and *Campodea* in one. Presumably these were washed into the stream.

Hemiptera Homoptera of three families, Aphididae, Psyllidae and Jassidae, occurred in 16 fish in September and October. Most were aphid nymphs of which up to seven occurred per fish, including some with attached parasitic hymenopteran coccoons, but three winged aphids, two adult jassids and an adult psyllid were also found.

Thysanoptera: two occurrences, one adult and one nymph.

Adult flies were found in 12 fish in several months of the year. Most were chironomids but one cecidomyiid was also eaten.

Lepidopteran larvae occurred in five fish during autumn and spring.

Algae were unimportant and occurred in only 15 fish; the quantity present was always small, and it seems that they were eaten only accidentally. The only genera eaten were *Spirogyra* and *Closterium*, the former occurring in 12 fish in June which were caught in a stagnant reach that was thick with the alga.

Higher plant tissue, although occurring in 23 fish, was rarely eaten in any quantity, and was presumably eaten accidentally. Most of it was apparently dead grass.

Mineral matter consisting of sand was found in only two fish. Detritus and unidentified matter was recorded from 12 fish; most of this was without visible structure.

It will be noted that although much of all this is in agreement with the findings of Blegvad (Table 6) some food items which were important in the Birket were absent from the diet of his fish. This may be merely a reflexion of difference in fauna between the localities, but it may equally represent a racial difference in selectivity such as is suggested for *Gasterosteus aculeatus*. Wolski (1927) has indicated that definite fresh water and brackish water forms of *Pygosteus pungitius* exist.

(*c*) *Food eaten by fish of different sizes*

Comparison of Tables 7 and 10 shows that, with the exception of algae, which were little eaten by *P. pungitius*, the changes in percentage composition of the food of growing *Gasterosteus aculeatus* and *Pygosteus pungitius* were almost identical. The remarks made above about *Gasterosteus aculeatus* therefore apply equally well to *Pygosteus pungitius*. It should be noticed, however, that as *P. pungitius* grows to a smaller size than *Gasterosteus aculeatus* the changes do not proceed so far. The high percentage of stickleback eggs and larvae shown as eaten by the 14-20 mm. size group of *Pygosteus pungitius* is due to the presence of one fish larva only and to the fact that only 10 such small fishes were examined. This paucity of numbers probably accounts also for the apparently great importance of copepods at this stage.

Unlike *Gasterosteus aculeatus* there appeared to be no correlation between size of fish and percentage of empty stomachs. *Pygosteus pungitius* shows generally higher percentages of empty stomachs and therefore appears to feed more sporadically than *Gasterosteus aculeatus* at all ages.

(*d*) *Seasonal variation*

For some unknown reason only eight fish were caught in early November, and at the end of that month none could be found. During December and January only two fish were taken, near the stream mouth. In early February only two fish were found, both near the stream mouth, but at the end of that month they occurred abundantly in mixed shoals of sticklebacks in the fresh water. It is accordingly not possible adequately to consider the seasonal feeding habits of this species. It is, however, possible to state that, unlike *G. aculeatus*, this species had not eaten large quantities of diatoms when it occurred in shoals in the autumn.

For comparison with *G. aculeatus*, Table 11 shows the average number of points allotted per fish and the percentage of fish with empty stomachs for the months for which adequate data are available. It will be seen that the general trend of the figures is similar to that of *G. aculeatus* (Table 9). There was a similar maximum of feeding activity in late summer and autumn, and there are indications of a winter minimum. The increase in percentage of fish with empty stomachs during the breeding season was also similar. There is, however, one difference between the two species.

Table 10. *The percentage composition of the food of* Pygosteus pungitius *from the Birket and the change in composition of the food with increase in size of the fish*

	Size groups					Total 656		
Number of fish	10	85	344	200	17	14–55		
Size range (mm.)	14–	20–	30–	40–	50–55			
Method of assessment	P	P	P	P	P	P	O	D
Food item								
Rotifera	+	+	.	.	.	+	+	.
Nematoda	.	.	+	.	.	+	+	.
Invertebrate eggs	.	.	+	+	.	+	+	+
Aquatic Oligochaeta	.	1	3	2	7	3	2	4
Sphaerium lacustre	.	+	5	1	1	3	2	3
Hydrobia jenkinsi	.	+	2	1	1	1	2	1
Other Mollusca	.	.	+	1	3	+	+	+
Hydracarina	.	+	+	.	.	+	+	.
Cladocera	23	11	11	9	+	11	16	9
Copepoda	53	38	21	14	10	22	22	24
Ostracoda	.	6	7	6	8	7	11	3
Higher Crustacea	.	21	20	18	20	19	13	20
Ephemeropteran nymphs	3	2	1	+	.	1	1	+
Aquatic Hemipteran nymphs	.	.	+	.	.	+	+	.
Trichopteran larvae	.	.	+	3	.	1	1	1
Aquatic Coleopteran larvae	.	.	1	+	.	+	1	+
Chironomid larvae	14	12	16	23	13	17	16	18
Chironomid pupae	.	3	6	11	17	7	5	9
Other Dipteran larvae	.	1	1	3	.	1	1	2
Unidentified Arthropoda	.	+	+	+	.	+	+	.
Stickleback eggs and larvae	5	.	1	1	4	1	1	1
Spiders	.	.	+	.	.	+	+	+
Collembola (and *Campodea*)	.	+	.	+	2	+	+	.
Homoptera	.	2	2	+	.	2	1	2
Thysanoptera	.	.	+	+	.	+	+	.
Dipteran adults	.	.	1	1	2	1	1	1
Lepidopteran larvae	.	.	+	1	8	+	+	+
Algae	.	+	+	+	.	+	1	.
Higher plant tissue	.	+	1	2	3	1	1	+
Mineral matter	.	.	+	+	.	+	+	.
Detritus, unidentified etc.	.	.	1	1	2	1	1	1
Fish with empty stomachs (%)	0	13	7	15	12		10	

P = points method; O = occurrence method; D = dominance mothod.

Table 11. *The amount of food taken month by month by* Pygosteus pungitius *in the Birket and percentage of fish with empty stomachs*

Month	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
No. of fish examined	37	4	64	79	169	8	1	1	29	87	98	79
Fish with empty stomachs (%)	5·4	0	4·7	1·3	7·1	0	0	0	13·8	24·2	18·4	6·3
Av. number of points per fish	16·6	17·5	18·6	17·5	12·0	13·1	(5·0)	(13·0)	15·4	10·0	9·3	15·7
Av. number of points per fish excluding fishes with empty stomachs	17·5	17·5	19·6	17·4	12·9	13·1	(5·0)	(13·0)	17·8	13·5	11·4	16·8

During the breeding season those specimens of *G. aculeatus* which contained food had fed heavily, and, as a result, the average number of points per fish excluding fishes with empty stomachs does not fall in March and April. In *Pygosteus pungitius*, on the other hand, this figure falls steeply from the February value, thus indicating that there was a general disturbance in feeding activity at this season. It is possible, however, that the February figure, which is based on 29 fish only, is too high. Even so, if the October value (169 fish) represents the winter level of feeding there was a distinct fall in feeding at this season. It was found that the average number of points gained in March and April was significantly lower than the number of points gained at other times of the year ($P < 0{\cdot}01$). It was also found that there was no

significant difference, at P 0·05, between the number of points gained by males and females at this season, showing that, as in *Gasterosteus aculeatus*, the disturbance in feeding at the breeding season affects both sexes alike.

6. *Parasites*

During the investigation notes were kept on parasites found infesting the fish. No examination of the intestine or gill chamber was made, so the following notes apply only to parasites of the skin, body cavity and stomach.

Table 12. *Numbers and percentages of fish with four types of parasite.* (*The numbers examined differ for each species of parasite because not all fish were opened and the stomachs of those that were opened were not all examined*)

		Glugea anomalum		*Schistocephalus solidus*		Unidentified plerocercoids		Gastric nematodes	
Species of fish	Locality	No. fish examined	No. (%) infected	No. fish examined	No. (%) infected	No. fish examined	No. (%) infected	No. fish examined	No. (%) infected
Gasterosteus aculeatus	Birket	2002	113 (5·6)	1828	30 (1·6)	1828	— (0)	1581	39 (2·5)
	Windermere	581	5 (0·9)	120	1 (0·8)	120	17 (14·2)	120	— (0)
	Easdale	55	— (0)	55	— (0)	55	— (0)	55	7 (12·7)
Pygosteus	Birket	687	3 (0·4)	656	1 (0·2)	656	— (0)	656	14 (2·1)

Table 12 shows the number of specimens infected and percentage infection by the four types of parasite found. The figures for the Birket are based on all months of the year.

Glugea anomalum (Monz.), a sporozoan (Neosporidia) which was identified from descriptions by Stempell (1904), caused white blisters on any part of the body surface. In the Windermere sample the blisters were small, and only one fish had two, but in the Birket up to seven large blisters occurred although one or two was the usual number. Infected fish were found in all months, and there was no seasonal maximum. Fish of all sizes from 20 mm. upwards were infected. It is noticeable that *Gasterosteus aculeatus* in the Birket was far more heavily infected than *Pygosteus pungitius*. The three infected fish of the latter species had only one small lesion each and were caught in August and October.

Schistocephalus solidus (Müll.), a cestode, was identified with the aid of keys in Joyeux & Baer (1936). The plerocercoids were found free in the body cavity of the fish and ranged up to 19 mm. long. Usually only one was present, but up to three were found. Larger numbers than this and much higher infestations are known to occur (Smyth, 1946). No fish smaller than 24 mm. was found infected, but the worms obviously grow rapidly because in September fish of 30 mm. and under, which we have found to be at most 7 months old, contained plerocercoids up to 14 mm. long. There seemed to be no seasonal maximum of infestation, and here also it is noticeable that in the Birket *Gasterosteus aculeatus* seems to be far more readily infected than *Pygosteus pungitius*. It was noticeable that no very small plerocercoids were found despite careful search; the smallest recorded was 6 mm. long in September.

Unidentified plerocercoids were found only in the fish from Windermere. These differed from *Schistocephalus* in being unsegmented and curled up in cysts in the stomach wall and liver. They were also considerably smaller (5 mm. and less). The largest specimens were wholly or partly free of the cysts. These plerocercoids occurred only in fish of at least 43 mm. length. Such fish were probably in their third winter. Up to 11 specimens occurred per fish, and of the fish over 43 mm. long which were examined 47 % were infected.

Gastric nematodes. The stomachs of many fish contained from one to five small nematodes, which showed no sign of being digested, and were presumably parasites. These nematodes were not identified, but certainly more than one species was present. There seemed to be no seasonal maximum, and in the Birket both species of stickleback were about equally infected.

D. FEEDING RELATIONSHIPS OF STICKLEBACKS AND ROACH (*RUTILUS RUTILUS* L.) IN THE BIRKET

Most of the sticklebacks studied were collected in the Birket, and as the only other fish present in any numbers in this stream were roach it was felt that an opportunity existed for a study of feeding relationships of an entire fish community similar to those made by Frost (1946*a*) and Hartley (1948). Accordingly, as many roach as possible were collected when netting for sticklebacks and the gut contents of these were examined.

1. *The food of* Rutilus rutilus *in the Birket*

Table 13 shows the percentage composition, based on the occurrence method, of the food of 236 roach caught in the Birket between early spring and late

Table 13. *The percentage composition of the food of* 236 Rutilus rutilus *from the Birket. Size range* 6–17 cm. *Percentage compositions based on occurrence method and examination of entire alimentary canal*

Food item	%
Oligochaeta	+
Sphaerium lacustre	3
Hydrobia jenkinsi	13
Limnaea pereger	+
Ostracoda	3
Higher Crustacea	4
Corixidae (adults and nymphs)	1
Trichoptera larvae	+
Aquatic Coleoptera	+
Chironomid fly larvae and pupae	5
Unidentified Arthropoda	3
Terrestrial Arthropoda	5
Algae	8
Higher plant tissue	24
Mineral matter	9
'Detritus'	21
Fish with empty stomachs (%)	31
Fish with entirely empty gut (%)	14

autumn; 31 of these fish were caught in one of the tributaries (Arrowe Brook).

The fish were preserved in formalin soon after netting. They were measured to the nearest centimetre below, the distance measured being from the tip of snout to the tip of the central tail fin ray. For reasons given above (section B) the occurrence method was used in assessing the food of these fish, and because of the high percentage with empty stomachs, and the limited number of specimens available, the entire contents of the alimentary canal were examined. Roach chew their food and mix it with much mucus, and this makes identification very difficult.

The food items need little comment. The one oligochaete found was a tubificid, the molluscs were of various sizes but very much broken; the ostracods occurred in small numbers; higher Crustacea were *Asellus* and *Gammarus*; the one caddis larva (*Limnophilus* sp.) had been eaten with its case; the aquatic beetles were adult Dytiscidae; terrestrial arthropods included various flies, beetles and Hymenoptera, the water-bug *Velia currens* and a spider; the algae were nearly all diatoms with a little filamentous algae; the higher plant tissue appeared to be mostly grass, but some *Elodea* was present. As in the stickleback the 'detritus' looked like higher plant tissue which was too much decomposed and finely divided to show structure. It usually occurred with higher plant tissue, and sand when present occurred with it. It seems therefore that these fish may eat much partly decayed plant tissue.

It will be seen that the food of these fish is very similar to that found by Hartley (1940, 1947) in some Cambridgeshire rivers and the Norfolk Broads. Hartley found, however, that the food of the younger fish was diatoms and planktonic Crustacea. No very small fish were found in the Birket, but the smallest (6 cm.), caught in October, were eating the same food as larger fish.

2. *The food of* Gobius minutus *L.*

For the sake of completeness the stomachs of the five gobies caught were examined. The fish ranged in length from 20 to 29 mm. The stomach of one was empty and the other four contained between 6 and about 40 small copper-blue Harpactoids quite unlike the *Canthocamptus* occasionally found in stickleback stomachs. One fish also contained an ostracod. This is in agreement with the statements of Day (1880–4) and Smitt (1892) that this species feeds on small Crustacea. It seems to be so rare in the Birket that it cannot be considered as a competitor for the available food.

3. *Comparison of the food of the principal species*

Fig. 1 shows the percentage composition of the food of both species of stickleback and of roach from the Birket. The occurrence method has been used for all three species to make the histograms strictly comparable. It will be seen that the diet of the two species of stickleback was remarkably similar, the only difference being that plants were slightly more important in the diet of *Gasterosteus aculeatus*. The roach, on the other hand, had fed mostly on vegetable matter and mollusca, and there is little overlap with the food of the sticklebacks. Such differences in diet of fishes feeding in the same habitat is sound evidence that they select their food and do not merely eat what is there. It can be assumed, therefore, that roach and stickleback do not normally compete for food in the Birket, although, as stated above, the very young roach may feed on small Crustacea. There are, however, so few roach that it is doubtful if true competition for food exists at any time. The numbers of roach are probably kept down partly by the small area of water available to them in drought periods, and partly by children.

The two stickleback species, on the other hand, appear to be in direct competition for food, and to form another pair of fish with almost identical feeding habits similar to the breams (*Abramis brama* L. and *Blicca bjoerkana* L.), and the perch and ruffe (*Perca fluviatilis* R. and *Acerina cernua* L.) (Hartley, 1947). It seems possible, however, that no such competition for food actually exists, and that the Birket's fauna, which has been shown to be very rich, is sufficient to support a normal concentration of both species. When, however, overcrowding occurs, as when the fish form large

shoals in autumn, food appears to become temporarily scarce (p. 49). It is well known that these two species differ greatly in breeding habits. These differences have been minutely tabulated by Leiner (1931), and they probably enable the two species to live together despite the fact that they exploit the same food supply. males at breeding time (Wunder, 1930; Tinbergen & van Iersel, 1947) probably regulates the number of each species present in the same manner as is known to occur in some birds. It seems, therefore, that the numbers are normally regulated before food becomes a limiting factor.

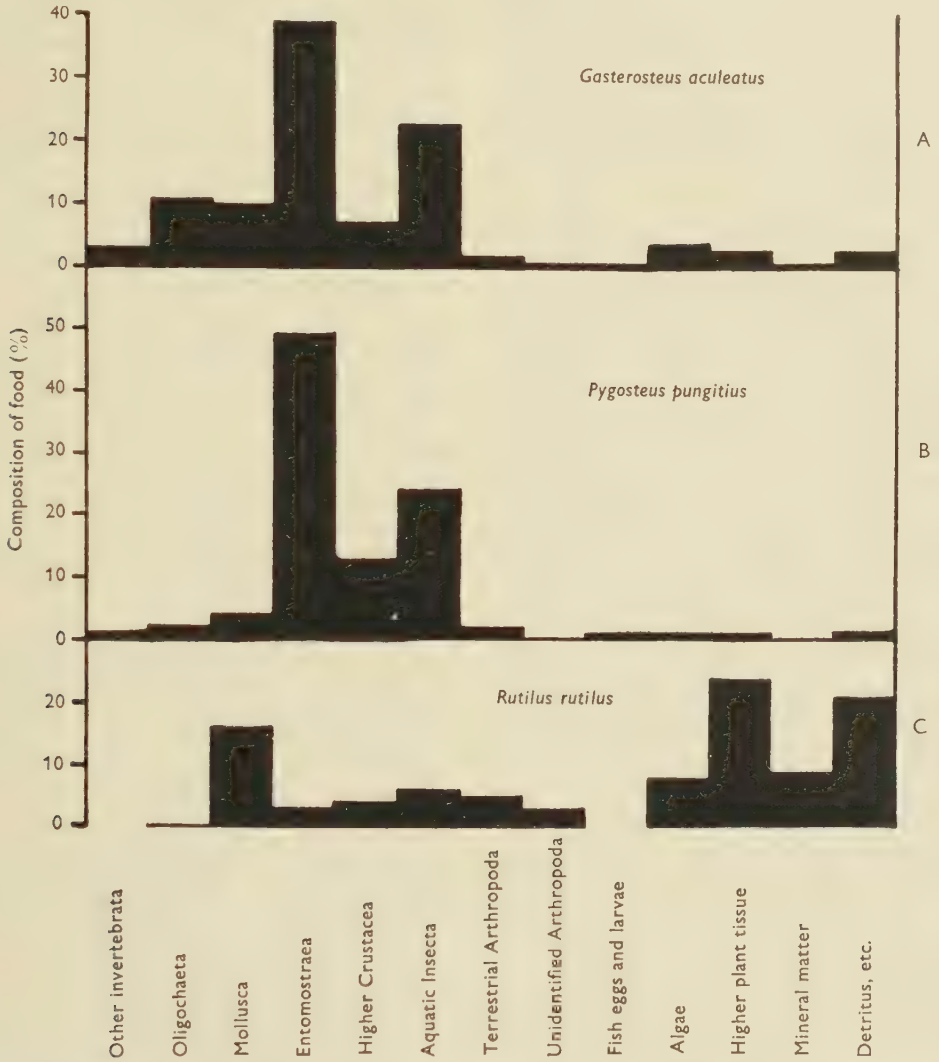

Fig. 1. Histograms showing the percentage composition of the food of the three principal species of fish inhabiting the Birket. A, *Gasterosteus aculeatus* (1581 fish). B., *Pygosteus pungitius* (656 fish). C. *Rutilus rutilus* (236 fish). All based on the occurrence method.

Gasterosteus aculeatus nests in open areas while *Pygosteus pungitius* nests in weeds, and the proportion of weeds to open areas probably regulates the proportion of the two species. Both species appear, however, to range over both types of habitat when not actually nesting. The territorial behaviour of the

Gasterosteus aculeatus is much more common in the Birket than *Pygosteus pungitius* and this is probably not only connected with the fact that more of the stream-bed is bare than is covered with weeds, but also with the fact that *P. pungitius* in the Birket seems to breed only in the fresh-water reaches, whereas

Gasterosteus aculeatus breeds everywhere where there is open unshaded bottom. Neither species appears to breed in shaded reaches nor in reaches choked with emergent vegetation. It should be noted, however, that *Pygosteus pungitius* breeds in the brackish water of the Baltic (Blegvad, 1917), and that it occurs in isolated brackish pools near the Birket and has done so for a long time (Forbes, 1897). It is certainly not therefore always confined to breeding in fresh water, and Wolski (1927) has shown that in Poland there are biometrical differences between *P. pungitius* from fresh and brackish water. The whole question of the relation between this species and the salt concentration of the water presents a problem for further investigation.

One interesting difference in feeding habits does, however, exist and that is the ability of *Gasterosteus aculeatus* to eat algae during periods of food shortage. This ability does not seem to be shared by *Pygosteus pungitius*, because, although admittedly this species was not adequately sampled during the winter, specimens from mixed shoals in the autumn were not found to have been eating algae, whereas specimens of *Gasterosteus aculeatus* from the same shoals had been eating large amounts. This may account at least in part for the fact that *G. aculeatus* occurs in almost all suitable ponds and streams, whereas *Pygosteus pungitius* is generally scarcer. One can suppose that, normally, when suitable nesting sites are available and other conditions such as food, current, temperature, etc., are suitable, both species occur together and regulate their numbers as suggested above. If for some reason such as drought or a series of particularly favourable seasons, overcrowding does occur, *Gasterosteus aculeatus* is more likely to survive the food shortage because of its flexible feeding behaviour. *G. aculeatus* does, however, seem to be more susceptible to infection by *Glugea anomala* and *Schistocephalus solidus*, and this perhaps is a factor in favour of *Pygosteus pungitius*.

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F. SUMMARY

1. The various commonly used methods of assessing, on the basis of gut contents, the food of those fishes which have a generalized diet are listed and discussed. Both during the present investigation and by re-examination of published data it is shown that, when a large number of fish are examined, and when the results are expressed comparably, i.e. each food item is shown as a percentage of the total food eaten, all methods give substantially the same results. Reasons are, however, given for rejection of the method based on the number of organisms eaten, and also of the practice of comparing data so obtained with counts of the organisms found in samples of small areas of the substratum. Such comparisons have in the past been used to give numerical expression to the availability of food organisms; but it is suggested that this would be better accomplished by using an arbitrary method of allocation of points on the basis of estimated volume of each food item present (*a*) in the fish guts, and (*b*) in general faunal collections from the habitat. The number of points, expressed as a percentage of the total, gained by any food item in the fish guts and in the general collections could then be compared.

2. The food of *Gasterosteus aculeatus* is studied, and it is shown that the diet, consisting chiefly of Crustacea and insects, changes slightly with season and with increase in size of fish. During the winter the fish eat less than at other times, and both sexes feed more sporadically than usual during the breeding season. It is suggested that the two biological races, *A* and *B* of Heuts, have different diets.

3. The food of *Pygosteus pungitius* is shown to be similar to that of *Gasterosteus aculeatus*, and to vary similarly. The data for the winter are, however, incomplete, and it appears that feeding in this species is more affected during the breeding season.

4. The food relations of three species of fish (*G. aculeatus*, *Pygosteus pungitius* and *Rutilus rutilus*) in a a small muddy Cheshire stream are discussed. It is shown that *R. rutilus* does not compete with the two other species, but that the diets of the two stickleback species are almost identical. It is suggested that differences in breeding habits enable these two species to live together as they nest in different areas, and that the number of each species is regulated by the fact that during the breeding season the males defend a definite territory round their nests. There is therefore only room for a certain number of nests of each species.

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THE AGE AND GROWTH OF *GASTEROSTEUS ACULEATUS*, *PYGOSTEUS PUNGITIUS* AND *SPINACHIA VULGARIS*, AS SHOWN BY THEIR OTOLITHS

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(With 3 Figures in the Text)

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A. INTRODUCTION

Little appears to be known about the ecology of the European fresh-water sticklebacks. As these fishes are common and widespread and important in the ecology of many bodies of fresh water, it was decided to investigate certain aspects of their life history. This is the second of two papers, the first of which (Hynes, 1950) dealt with the food of *Gasterosteus aculeatus* L. and *Pygosteus pungitius* (L.).

This paper is concerned primarily with the age and growth of *Gasterosteus aculeatus* and *Pygosteus pungitius*, but it includes the study of a few *Spinachia vulgaris* Fleming.

B. REVIEW OF THE LITERATURE

1. *The age of sticklebacks*

Several authors have commented on the length of life of the three European species of stickleback; but there is little agreement in the estimates which have been made except for those relating to *Spinachia vulgaris*.

(*a*) *Gasterosteus aculeatus*.

Lacépède (1802), Day (1880–4), Smith (1892) and other early authors state that *G. aculeatus* lives for 3 years or longer.

Bertin (1925), after a statistical study of size distribution in samples of fish taken at various seasons in many places in France and the Netherlands, concludes that the fish in these regions live for only two summers and die after breeding. His conclusions are based on the unimodal size distribution of nearly all his samples, but some of the samples showed more than one peak in size distribution, and he suggests that in some localities the fish may live for more than two summers. In support of his conclusion that the fish die after breeding he quotes Warington (1855), who was unable to keep these fish alive in an aquarium after breeding.

Croser (1928) showed that it was possible for fish kept under good aquarium conditions to recover after breeding, and Bock (1928) estimated that specimens of the race *gymnura* from Germany live in aquaria for at least 3 years and probably up to 5. He examined the otoliths, and concluded that these did not always suffice for accurate age determination. When, however, the otolith readings were combined with size and weight of the fish it was usually possible to determine age. Unfortunately, Bock gives no details of his otolith technique. He found that 1-year-old fish were *c.* 3·5–4·0 cm. long, 2-year-old *c.* 4·5 cm. and 3-year-old *c.* 5·0–5·5 cm.; the maximum size attained was 6·0 cm.

Craig-Bennett (1931), who investigated the race *gymnura* in Britain, points out that the growth rate in aquaria varies considerably, and gives a table showing the rate of growth of two fish up to the age of 5 months, when they measured 3·1 and 2·6 cm. He also shows that the growth rate in larger fish is much slower:

a 4·6 cm. fish only grew to 4·9 cm. in 10 months. Males in his field population did not become mature until they were 4·5 cm. long, and he concludes therefore that they do not breed in their second summer. He also states that it is possible histologically to distinguish fish which have spawned from those which are mature for the first time. He therefore implies that the fish live for at least 3 years. Fish from his population rarely exceeded 5·5 cm. in length.

Wunder (1928, 1930), working in Germany apparently on the race *trachura* as shown by his figures, found that in aquaria these fish die in their fourth year. He found that the three recognizable year groups were 3, 5 and 7 cm. long respectively at the end of the first, second, and third years of life. Yearling fish did not breed, but some well-fed fish grew to 7 cm. in 6 months. Heilborn (1931), who quotes Wunder's work, states that wild fish live not more than 4 years.

Leiner (1930, 1931, 1934) in Germany, also apparently working with the race *trachura* as shown by his figures, reached similar conclusions based on observations on fish in aquaria. He states, however, that yearlings will breed, and found it impossible to distinguish year groups by means of length-frequency distribution because of the great variation in the growth rate. Fish below 4·5 cm. long were found to be rare in the field in early spring, and the largest fish taken were 7·8 cm. long.

Heuts (1947*a*, *b*) accepts Bertin's conclusion that the fish live for only 1 year, and uses mean size of the fish as one of the differentiating characters between two types of population in Belgium.

There is therefore little agreement as to the length of life and rate of growth of *G. aculeatus*, although the most widely accepted opinion is that they live for 3 or 4 years and may not breed during their first year. All authors are agreed that the breeding season is the spring.

(*b*) *Pygosteus pungitius*

Bertin (1925) believes all species of stickleback to be annual fish, but Leiner (1934), working in Germany, states that *P. pungitius* lives for two or three breeding seasons. Bertin is of the opinion that breeding occurs in the spring, but Leiner found that, in aquaria, this species will also breed in the autumn, and that some fish will breed when only 3 or 4 months old. He found that growth was rapid, some fish reaching 5·6–5·9 cm. in 7 months. Leiner did not confirm autumn breeding in the field but concludes that as this species grows so quickly, small fish caught in the spring are the product of autumn spawning. Specimens from 2·4 to 7·6 cm. long were recorded in early spring. The autumn breeding of *P. pungitius* has not been verified by any other investigator.

(*c*) *Spinachia vulgaris*

Petersen (1893) states that *S. vulgaris* lives for only 1 year in Danish seas, breeding during May and dying in July. The fish are 3–8 cm. long in August, 8–13 cm. in September, 12–18 cm. in November and 13–19 cm. in May. Bertin (1925), Scheuring (1930) and Leiner (1934) support this statement, but Smitt (1892) implies that they may live longer than 1 year.

2. *The use of otoliths in age determination of some fishes*

As stated below, otoliths were found to be the only satisfactory method of determining the age of sticklebacks. There are usually three otoliths found in the auditory organs of fishes, the sagitta, astericus and lapillus (Parker & Haswell, 1928). The sagitta is the largest and is the one that has usually been used for age determination. When examined under the microscope by transmitted light, otoliths generally show alternating bands which have been variously termed light and dark, opaque and transparent, white and translucent, etc. In the present investigation the rings are termed opaque and transparent, as these terms are independent of the illumination used. When otoliths are examined by reflected light against a dark background the opaque bands appear white and the transparent bands black.

Reibisch (1899) is of the opinion that in the otoliths of *Pleuronectes platessa*, when examined under transmitted light, the light (transparent) ring represents the 'summer' growth, and the dark (opaque) ring represents the 'winter' growth, the latter being formed in January and February. Jenkins (1902), also using transmitted light, found that in the otoliths of *Clupea harengus*, *C. sprattus* and *C. pilchardus* the light (transparent) ring was formed in summer, and the dark opaque ring in January to February. Cunningham (1905), who examined the otoliths of plaice by transmitted light, concluded that the opaque ring was formed in summer and the transparent zone in March to April. From his description there seems little doubt that this opaque zone is the same as the dark zone described by Reibisch. Wallace (1907) who also examined the otoliths of plaice, under reflected light, found that the white (opaque) bands were formed in spring and summer, and the dark (transparent) bands in autumn and winter. Maier (1908) found that in the otoliths of *Pleuronectes microcephalus* white (opaque) bands were formed in April to June and dark (transparent) bands in July to November; there was no otolith growth from December to March.

Conolly (1922) describes bright (transparent) summer rings and dark (opaque) winter rings in the otoliths of *Lophius piscatorius* as seen by transmitted light.

Bertwistle & Lewis (1923) found opaque summer

and clear (transparent) winter rings in the otoliths of *Clupea harengus* examined by transmitted light. Lissner (1925), using the same form of illumination, states that the opaque rings were formed in May–July on the otoliths of *C. harengus*, and the hyaline (transparent) rings were formed from August to April.

Hickling (1933), working on *Merluccius merluccius*, found that the narrow translucent (transparent) zone was formed during August to October and the opaque during the other months. Frost (1945), who quotes other workers on eel otoliths, found that in *Anguilla anguilla* the white opaque band was laid down in summer (August to November) and the dark and comparatively translucent band in winter. Hickling and Frost used reflected light.

In the present investigation, in which reflected light was used, the transparent (dark) zone was formed only during the period June to September inclusive.

The 'seasonal' nature of the bands as deduced by workers to date can therefore be interpreted as follows:

Fish	Ring formation: Transparent	Ring formation: Opaque	Investigator
	(*a*) Marine		
Pleuronectes platessa	Winter—March, April	Summer	Cunningham
P. platessa	Autumn, winter	Spring, summer	Wallace
P. microcephalus	Winter—July to November	April to June	Maier
Merluccius merluccius	August to October	Other months	Hickling
Pleuronectes platessa	Winter—March, April	Summer	Cunningham
Lophius piscatorius	Summer	Winter	Conolly
Clupea harengus	Winter	Summer	Bertwistle & Lewis
	(*b*) Fresh water		
Anguilla anguilla	Winter	August to November	Frost
Gasterosteus aculeatus, *Pygosteus pungitius*	June to September (inclusive)	Other months	Present investigation

The conflicting statements of Reibisch are not included above. The transparent band, therefore, can be formed on otoliths in almost any month of the year, dependent on the species, and cannot truly be termed a winter band. Thus otoliths, like scales, can only be used for age determination of fishes in conjunction with other biological facts relating to the species being investigated (cf. Van Oosten, 1941).

C. MATERIAL INVESTIGATED

The seasonal changes in otoliths were determined by examination of successive monthly samples of *Gasterosteus aculeatus* and *Pygosteus pungitius*. These samples were collected during the period June 1947 to June 1948, from the Birket, a small muddy stream on the Wirral peninsula of Cheshire, which has been described by Hynes (1950).

The fish were caught with a small seine net made of mosquito netting, or with two similar short nets which were placed across the stream and brought together before being lifted. As it was usually necessary to net several times in order to obtain sufficient fish, it is probable that random samples of the fish population were caught.

Monthly samples of *Gasterosteus aculeatus* contained from 24 to 412 fish (Table 1), but the numbers of *Pygosteus pungitius* varied from 4 to 166, and during December and January none were obtained (Table 2). The reason for this is unknown as these fish were readily obtainable in January 1949, and failure to catch them in the winter of 1948 may have been entirely due to difficulties of netting during the high water of that year.

In addition, a sample of 582 *Gasterosteus aculeatus* taken with a seine net in Windermere, Westmorland, in November 1947, and 27 *G. aculeatus* caught by rod and line in a brackish quarry on Easdale Island, Argyllshire, during June 1948, were examined. The latter sample did not contain any of the small fish hatched in 1948, which were presumably present.

Five specimens of *Spinachia vulgaris* caught in the sea near Great Cumbrae, Argyllshire, during December 1948 were also examined.

The races of *Gasterosteus aculeatus* have been described by Bertin (1925) and Heuts (1947*b*). The *G. aculeatus* from the Birket all belonged to race *gymnura*, or type A^m of Heuts, those from Windermere were mostly *gymnura*, with a few (5 %) *semiarmata* or type A^i of Heuts, and so belonged, as did those from the Birket, to race *A*. The *G. aculeatus* from Easdale were all of race *trachura*, or type B^m of race *B*, and the fish from this locality are peculiar in that they grow to a very large size.

The *Pygosteus pungitius* all belonged to the races *hologymna* and *carinata* (Bertin, 1925), only the largest specimens bearing a caudal keel.

D. METHODS

1. *Preservation*

The fish were preserved in the field and usually examined within a few days of capture, although some samples were kept for 3 weeks before examination. The samples were preserved in alcohol, as formalin, even when neutralized, dissolved the otoliths after 2–3 weeks.

2. *Measurement*

The fish were measured from the snout to the tip of the middle tail fin ray, the length being recorded to the nearest millimetre below. As, however, some authors (Leiner, 1930, 1931, 1934; Heuts, 1947*a*) have recorded lengths measured from the snout to the base of the tail, several hundred specimens of *Gasterosteus aculeatus* and *Pygosteus pungitius* were measured by both methods, the lengths being recorded to the nearest quarter millimetre. From these measurements it was found graphically that, for *Gasterosteus aculeatus*, length to base of tail = 0·90 length to tip of middle fin ray, and that for *Pygosteus pungitius* the factor was 0·88. These factors apply to all fish from 10 mm. overall length, at which size the tail is fully developed, to 96 mm. for *Gasterosteus aculeatus* and to 55 mm. for *Pygosteus pungitius*, as growth of the tail is isogonic.

3. *Extraction and treatment of otoliths*

Stickleback have no scales and analysis of size distribution gives anomalous results (Bertin, 1925). Thus other structures were examined for evidence of annual rings. The bony lateral scutes showed none, although some opercular bones showed vague annulations, which could only be made out in reflected light. It was therefore not possible to use the technique which Le Cren (1948) has applied to study of the perch. Otoliths, however, showed definite annulations, and the investigation was confined to study of these, despite difficulties in extraction from small fish and in interpretation.

All three otolith pairs are present in stickleback, but only the largest, the sagittae, was found to be of use in age determination. Both sagittae were removed from each fish as follows. The top of the cranium was sliced off with a sharp scalpel, the cut extending from just behind the top of the head to the back of the eye. The fish was then pinned down under water and examined under a low power binocular microscope. The sagittae were exposed by removal of the remains of the medulla oblongata and picked out with fine forceps. They were placed in water in a watch-glass, cleared of remnants of the sacculus with fine needles and transferred first to absolute alcohol for 3–5 min. and then to pure creosote for about 5 min. The otoliths were mounted in canada balsam as they were very small and easily lost. Other clearing agents, including xylol, phenol and amyl acetate were tried, but creosote, which has been recommended for otoliths both by Johnston (1938) and Frost (1945), was found to be the most satisfactory.

This technique was found satisfactory for fish of all sizes, and after the first hundred and fifty fish almost 100% of the otoliths were extracted without loss, although occasionally only one otolith was finally mounted. The two otoliths gave identical readings in over 95% of the 500 or so pairs checked; in all cases where they did not agree one of the otoliths was unreadable.

Some of the otoliths of large *Gasterosteus aculeatus* were found to be more easily read after slight grinding (Frost, 1945).

E. DESCRIPTION OF OTOLITHS

The sagitta of all three species of stickleback is roughly lens-shaped with a V-shaped notch at one side. In large specimens the edge tends to be crenulated. When examined by microscope by transmitted or polarized light, the rings are very vague, but by reflected light against a matt black background alternate light (opaque) and dark (transparent) concentric rings are much more clearly discernible in the otoliths of *G. aculeatus* and *Pygosteus pungitius*. No rings are visible in the otoliths of *Spinachia vulgaris*.

The core of the otolith may be either transparent or opaque, and outside this is an opaque zone in which one or sometimes two narrow transparent rings may be visible. This zone, hereinafter called the centre, is bounded by a clearly marked transparent ring which again is bounded by an opaque zone. As many as four transparent rings may be present, alternating with opaque zones. When an opaque zone forms the periphery, the extreme edge often appears to be transparent as the edge of the otolith is thin, but it is usually not difficult to distinguish this false transparency from the true transparent ring as in the former there is no relatively sharp boundary between the transparent and opaque areas, and the quality of the transparency is different. Similarly, the presence of high-lights at the extreme edge occasionally gives the impression that otoliths bear a narrow opaque zone at the edge, these were also mentioned by Wallace (1907). Here also practice enables one to determine which is the true opaque zone at the edge. Owing, however, to the thinness of the edge of the otolith it seems probable that a very narrow opaque zone at the edge would not be readily discernible.

In some otoliths narrow, often incomplete, transparent rings, similar to those often found in the centre, are visible, in the opaque zones between the more

definite transparent rings, and in a few specimens these are so well developed that 'multiple ring' otoliths of the type figured by Frost (1945) in the eel result. These are perhaps similar to the 'checks' found on some fish scales and the 'disturbance rings' on the shells of some molluscs which have been discussed by Jones (1949). We have, however, no evidence on this point. Occasionally single otoliths are almost entirely opaque so that few or no transparent rings can be made out, but in these instances the second otolith frequently shows the rings more clearly. Hickling (1931) has shown that the rings seen in the otoliths of hake are due to alternating layers of thick and thin organic lamellae embedded between radially arranged inorganic crystalline material, but he has offered no explanation of the cause of alternation of lamination.

F. INTERPRETATION OF OTOLITHS OF *GASTEROSTEUS ACULEATUS* AND *PYGOSTEUS PUNGITIUS*

It was found that with practice most otoliths, or at least one of the pair, could be interpreted, and that subsidiary transparent rings could be distinguished from the main ones. Only 8 (0·36%) of the 2227 *Gasterosteus aculeatus*, and 10 (1·53%) of the 655 *Pygosteus pungitius* examined were classified as having both otoliths unreadable because of opacity or multiple rings.

Gasterosteus aculeatus and *Pygosteus pungitius* were found to breed in April and May in the Birket, and there was no evidence of successful breeding in other months, although some specimens of *Gasterosteus aculeatus* were found still to be fully coloured or full of ripe eggs as late as July.

The sagitta first appears when the fish is about 6 mm. long, i.e. a few days after its emergence from the nest; the otolith is then a small body either uniformly transparent or more or less opaque. By the end of June the centre is usually completely formed. Otoliths in this state or in an earlier state of development were designated S −. During June or early July the first transparent (S) ring appears, followed by the opaque zone (+), which is visible in some fish in July and in all by September. At first the opaque zone is narrow, but it rapidly increases in width during the summer. From September until the following June the otoliths of all fish in their first year read S+, i.e. they consist of centre, one transparent ring and an opaque zone. Thereafter the S ring becomes evident in July, not June or July as in young fish: this may be due to the fact that it is not so easy to see the S ring on the edge of the larger otoliths. The opaque zone (+) begins to be visible in August or September, and is present in all fish by October. No fish was found to have an otolith with more than four S bands. Those with four bands were all taken during the summer (July and September), thus indicating that it is unlikely that any fish survive into a fourth winter. It was possible therefore to classify otoliths as S−, S, S+, 2S+, 3S, 3S+ and 4S; the symbols used to describe otoliths are defined below.

S−, otolith with centre only (no transparent rings).

S, otolith with centre and one transparent ring at the edge.

S+, otolith with centre, one transparent ring and an opaque zone at the edge.

2S (S+S), otolith with centre, two transparent rings one forming the edge.

2S+ (S+S+), otolith with centre, two transparent rings and an opaque zone at the edge.

3S (S+S+S), otolith with centre, three transparent rings one forming the edge.

3S+ (S+S+S+), otolith with centre, three transparent rings and an opaque zone at the edge.

4S (S+S+S+S), otolith with centre, four transparent rings, one forming the edge.

Table 1 and 2 show the percentage of *Gasterosteus aculeatus* and *Pygosteus pungitius* from the Birket placed in each otolith group during every month in which samples were collected, and Fig. 1 shows how the readings of *Gasterosteus aculeatus* were interpreted as year groups. It will be seen that group S− occurred only during and just after the breeding season, that group S occurred only from June or July to September, and that groups 2S, 3S and 4S occurred only in July to September. Groups S+, 2S+ and 3S+ occurred in almost all months, although 2S+ 3S+ were relatively scarce in summer. This indicates that the transparent S ring begins to be laid down in June or July and that the opaque + zone begins to be laid down in July and is present in all fish by October. Comparison of Tables 1 and 2 indicates that *Pygosteus pungitius* follows the same cycle as *Gasterosteus aculeatus*, although this is less obvious because of the small numbers and the very small July sample.

It is therefore possible, knowing both the otolith reading and the month of capture, and assuming that, as is generally accepted (Bertin, 1925), the breeding season is the spring, to state the age of a stickleback to within 2 or 3 months. Similar arguments have been used by Hartley (1947) for the interpretation of roach scales.

The otoliths increase in size with the size of the fish, but the otoliths of large fish are relatively smaller than those of small fish. Their growth is therefore heterogonic. The breeding season is protracted, and great variations in individual growth rates occur (Craig-Bennett, 1931; Leiner, 1934), with the result that there is considerable variation in size of the fish, and consequently of their otoliths, at the time when the first S ring begins to form, in late June or early

July. A considerable variation in the size of the centre thus results.

No physiological explanation is offered for the appearance of the transparent rings nor of the 'false' rings which are often present in the centre and outer opaque zones.

Table 1. *Percentage of each otolith group in random monthly samples of* Gasterosteus aculeatus *from the Birket* (1947–8)

(The horizontal line below June represents the time at which it appears that formation of the new S ring begins in fish aged more than 1 year.)

Month of capture	No. of fish	Otolith readings (%)								
		S−	S	S+	2S	2S+	3S	3S+	4S	Unreadable
1947										
June	90	32·2	13·3	8·9	.	18·9	.	24·4	.	2·2
July	112	.	32·2	27·6	15·4	2·7	15·4	.	5·4	1·8
Aug.	83	.	56·6	38·6	2·4	.	1·3	1·3	.	.
Sept.	412	.	11·7	64·5	8·8	0·2	11·9	0·5	1·7	0·4
Oct.	89	.	.	67·4	.	16·9	.	15·7	.	.
Nov.	99	.	.	54·5	.	30·3	.	15·2	.	.
Dec.	114	.	.	63·3	.	28·9	.	7·0	.	0·9
1948										
Jan.	24	.	.	79·3	.	12·5	.	8·3	.	.
Feb.	89	.	.	34·9	.	48·4	.	16·7	.	.
Mar.	101	.	.	52·5	.	32·7	.	14·8	.	.
April	97	.	.	53·7	.	28·9	.	17·5	.	.
May	257	67·0	.	19·1	.	8·2	.	5·8	.	.
June	51	58·8	.	29·4	.	5·9	.	3·9	.	1·9

Table 2. *Percentage of each otolith group in random monthly samples of* Pygosteus pungitius *from the Birket* (1947–8)

(The horizontal line below June represents the time at which it appears that formation of the new S ring begins in fish aged more than 1 year.)

Month of capture	No. of fish	Otolith readings (%)								
		S−	S	S+	2S	2S+	3S	3S+	4S	Unreadable
1947										
June	31	6·5	.	9·7	.	51·7	.	25·8	.	6·5
July	4	.	100	.	.	.	.	.	.	.
Aug.	63	.	31·8	30·1	19·0	3·2	9·5	1·6	1·6	3·2
Sept.	73	.	.	46·6	1·3	37·0	4·1	8·2	.	2·7
Oct.	166	.	.	55·4	0·6	39·9	.	3·0	.	1·2
Nov.	8	.	.	37·5	.	50·0	.	12·5	.	.
Dec.	.	.	.	.	.	.	.	.	.	.
1948										
Jan.	.	.	.	.	.	.	.	.	.	.
Feb.	26	.	.	34·3	.	46·3	.	15·8	.	3·8
Mar.	82	.	.	23·2	.	53·7	.	23·2	.	.
Apr.	101	.	.	25·8	.	52·5	.	21·8	.	.
May	54	.	.	31·5	.	51·8	.	16·7	.	.
June	37	54·2	.	27·0	.	10·8	.	5·4	.	2·7

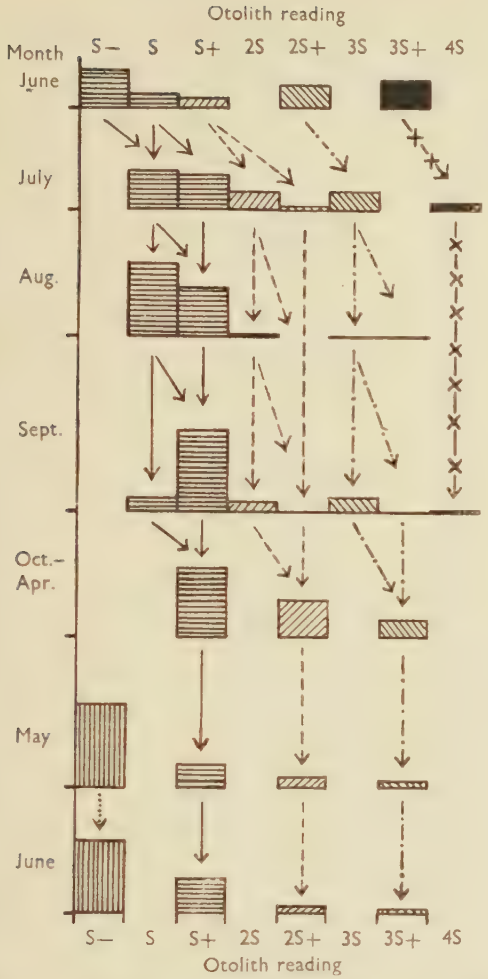

Fig. 1. Percentage of each otolith group in samples of *Gasterosteus aculeatus* from the Birket during June 1947 to June 1948. The shading and arrows denote the change over in otolith reading which occurs during the summer. October to April fish have been grouped together as no significant otolith changes take place during this period (cf. Table 1).

G. AGE AND GROWTH IN THE THREE SPECIES

1. *Gasterosteus aculeatus*

Table 3 shows the monthly mean sizes of the year groups, as determined by otolith readings of *G. aculeatus* taken in the Birket between June 1947 and June 1948. It is seen that no fish of the 1944 hatch, i.e. in their fourth year, were found after September, this indicating that this species probably does not live for more than about $3\frac{1}{2}$ years. The numerically small samples in some months produce irregularities, but it is seen that growth occurred in all age groups during the year. For any given age group the size attained by June 1948 was greater than that in June 1947. This indicates that growth was better during 1947–8 than it was during 1946–7. This is almost certainly the result of the severe winter of 1946–7 and the relatively late spring of that year.

An effort to smooth out the irregularities in Table 3 has been made by grouping the samples into four quarterly totals, and calculating the mean length for each age group. In calculating these means all the available data have been used; for instance in calculating the mean length of first year fish for the June quarter, all fish in their first year taken in June and July 1947 and May and June 1948 have been included, although these fish belong to two separate hatches. Therefore all means for the June quarters are composite, but for other quarters they are not. These means, and the maximum and minimum lengths during each quarter are shown in Table 4 and Fig. 2. In this figure a hypothetical source to the curve has been added by assuming that hatching occurs at the end of April; newly hatched fish are about 5 mm. long. It will be seen that even during the first 3 months of life some first-year fish grow to a length as great as that of the smallest second-year fish, that growth is rapid during the first year and then falls off, and that during the last 6 months of the maximum life span there is a fall in the mean size. This is probably because faster growing fish have a shorter life span than those growing slowly, but it may be due to a slower growth rate of fish hatched in 1944 than of fish hatched in 1945.

The fall in mean length of fish in their second year between the June and September quarters is an artefact, due to the composite nature of the June mean. It might have been expected that a similar rise in mean length would occur in the third year June quarter mean, but this is not so as the difference in size between 2-year-old fish in June 1947 and June 1948 was much less marked than it was for 1-year-old fish, due to the slower growth rate in later years of life. A similar explanation does not account for the fall in mean size at the end of the life span, discussed above, which may be a natural phenomenon.

It seems, therefore, that *G. aculeatus* in the Birket has a high growth rate in the first year, and that after only about the first 3 months of life the largest fish are at least as large as the smallest second-year fish. Thereafter, growth is slower and thus the overlap in size of the various year groups is almost complete. It also appears possible that towards the end of life, at about the third breeding season, the larger fish die off before the smaller ones, some of these smaller fish surviving until the following September. Prof. J. H. Orton, F.R.S., informs us that this is a common phenomenon in molluscs.

Table 3. *Average monthly lengths (mm.) of* Gasterosteus aculeatus *hatched in* 1944–8, *in samples taken from the Birket, June* 1947 *to June* 1948

Months ...	1947														1948											
	June		July		Aug.		Sept.		Oct.		Nov.		Dec.		Jan.		Feb.		Mar.		Apr.		May		June	
Year of hatching	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length
1944	22	49·8	6	43·5	.	.	7	45·6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1945	17	43·8	17	43·2	2	44·5	51	46·0	14	50·8	15	50·7	8	57·4	2	54·0	15	57·1	15	56·9	17	60·2	15	56·5	2	54·0
1946	8	34·2	20	36·8	2	27·0	37	39·1	15	44·6	30	41·7	33	42·2	3	34·4	43	43·9	33	43·6	28	49·6	21	50·0	3	46·7
1947	41	17·3	67	20·8	79	21·6	315	28·3	60	27·6	54	33·8	72	30·5	19	28·3	31	33·1	53	37·8	52	36·8	49	45·5	15	45·9
1948	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	172	11·0	30	22·4

Table 6. *Average monthly lengths (mm.) of* Pygosteus pungitius *hatched in* 1944–8, *in samples taken from the Birket, June* 1947 *to June* 1948

Months ...	1947														1948											
	June		July		Aug.		Sept.		Oct.		Nov.		Dec.		Jan.		Feb.		Mar.		Apr.		May		June	
Year of hatching	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length	No.	Av. length
1944	8	41·0	.	.	1	38·0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1945	16	38·6	.	.	7	39·1	9	39·2	5	40·2	1	40·0	.	.	.	.	4	38·2	19	46·7	22	47·5	9	48·4	2	45·0
1946	3	39·0	.	.	14	32·7	28	34·4	67	36·2	4	40·0	.	.	.	.	12	39·7	44	41·2	53	41·4	28	43·9	4	38·8
1947	2	20·0	4	25·8	39	23·3	34	28·8	92	31·9	3	34·7	.	.	.	.	9	32·8	19	37·6	26	38·2	17	39·8	10	40·8
1948	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	22·0

Table 4. *The mean quarterly length of* Gasterosteus aculeatus *from the Birket throughout the maximum life-span of a fish*

Year of life	Quarter	No. of fish examined	Extreme lengths (mm.) Min.	Max.	Mean length (mm.)
1	May–July	310	6	30	15·0 ± 0·32
	Aug.–Oct.	454	14	44	27·1 ± 0·21
	Nov.–Jan.	145	18	45	31·4 ± 0·40
	Feb.–Apr.	136	18	48	36·3 ± 0·50
2	May–July	92	27	53	42·7 ± 0·59
	Aug.–Oct.	54	27	54	40·2 + 0·83
	Nov.–Jan.	66	29	51	41·6 ± 0·66
	Feb.–Apr.	104	31	54	44·6 ± 0·48
3	May-July	58	35	56	45·6 ± 0·72
	Aug.–Oct.	67	44	56	47·1 ± 0·28
	Nov.–Jan.	25	41	62	53·1 ± 1·13
	Feb.–Apr.	47	49	73	58·2 ± 0·99
4	May–July	45	35	65	51·4 ± 1·04
	Aug.–Oct.	7	43	51	45·6 ± 1·21

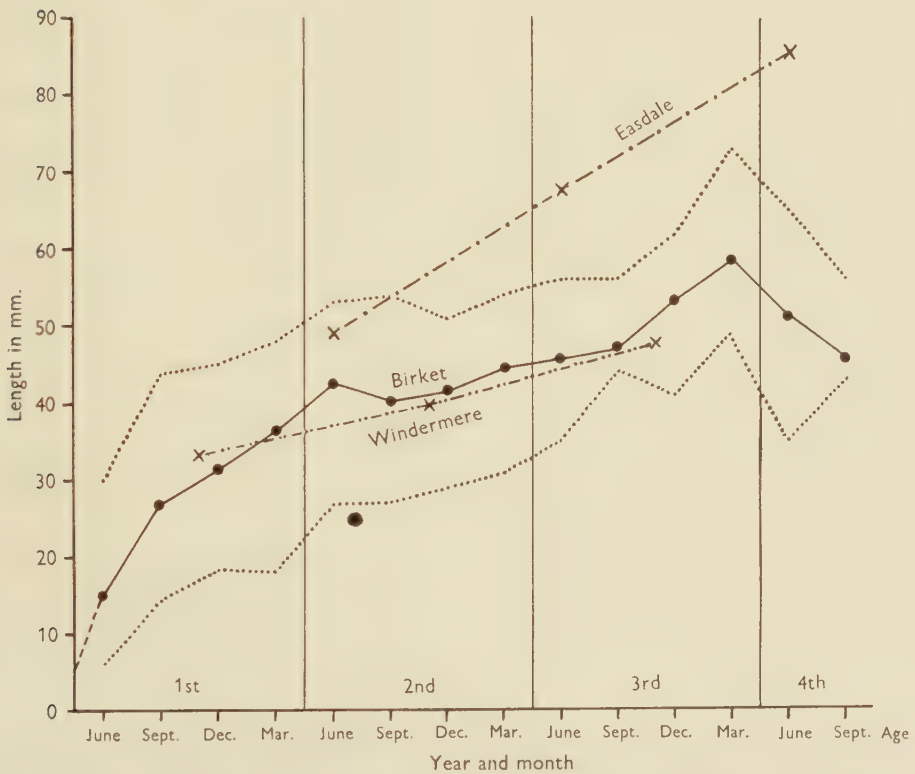

Fig. 2. *Gasterosteus aculeatus*: average length in each quarter of 1610 fish from the Birket, and average lengths of three year groups from Easdale (27 fish in June 1948) and from Windermere (582 fish in November 1947). The dotted lines represent the maximum and minimum lengths of the Birket fish, and the vertical lines denote the approximate times of breeding.

Table 5. *Age and length-distribution of four samples of* Gasterosteus aculeatus

Sample	Total no. of fish	Year group	No. of fish in each length group: Length groups in mm.																						
			10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
Birket, May 1948	257	0 (S−)	28	18	15	18	22	10	2	2	1	1	.	1	.	.	.	.	.	.	.	.	.	.	
		1 (S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
		2 (2S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
		3 (3S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Birket, Sept. 1947	410	1 (S, S+)	.	.	.	.	.	.	.	.	1	.	1	1	18	17	8	14	29	33	33	35	36	27	
		2 (2S, 2S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	
		3 (3S, 3S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
		4 (4S)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Windermere, Nov. 1947	582	1 (S+)	.	.	.	.	.	.	.	.	.	.	.	1	2	1	2	1	3	9	10	17	21	20	
		2 (2S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	3	
		3 (3S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
		Total	.	.	.	.	.	.	.	.	.	.	.	1	2	1	2	1	3	9	10	17	25	23	
Easdale, June 1948	27	1 (S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
		2 (2S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
		3 (3S+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

Sample	Year group	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Birket, May 1948	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1	.	.	.	.	1	.	.	1	2	2	2	3	7	9	3	6	4	4	4	.	1	.
	2	.	.	.	.	.	.	.	1	.	2	2	.	1	1	2	2	2	.	.	2	1	.
	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	.
Birket, Sept. 1947	1	30	15	13	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	2	1	1	4	4	2	1	6	4	2	1	1	2	2	1	.	.	.	.	1	1	.
	3	.	.	.	.	.	1	.	.	3	2	11	.	1	4	9	2	4	3	2	2	4	2
	4	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.	.	1	.	1	.	.
Windermere, Nov. 1947	1	30	25	22	39	33	22	18	12	5	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	2	5	5	7	9	20	17	19	31	31	24	22	12	13	1	3	1	2	.	.	.	.
	3	.	.	.	.	.	.	.	.	.	.	1	3	3	5	9	7	10	4	12	2	1	1
	Total	32	30	27	46	42	42	35	31	36	31	25	25	15	18	10	10	11	6	12	2	1	1
Easdale, June 1948	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	1	1	.	2
	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Sample	Year group	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Birket, May 1948	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	1	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	1	2	1	3	.	1	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.
Birket, Sept. 1947	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Windermere, Nov. 1947	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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	Total	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Easdale, June 1948	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	1	2	.	.	.	.	1	1	.	.	2	.	.	1	.	2	.	4	.
	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1

Sample	Year group	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
Birket, May 1948	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Birket, Sept. 1947	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Windermere, Nov. 1947	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Total	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Easdale, June 1948	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	1	.	.	1

Table 5 shows the overlap in length of the various year groups in several samples as determined by otolith readings, and it also explains how Bertin (1925) was misled into the belief that this species lives for only two summers by basing his investigations on size distribution alone. The length distribution of the fish from Windermere (Table 5) shows clearly how three overlapping year groups can produce a total size distribution which has the appearance of a normal distribution about one mean. This table also analyses the lengths of some Birket fish, and it is seen that all age groups were larger in May 1948 than they were in September 1947, even though in the September sample the fish were about 4 months older. The fact that growth in 1947–8 was better than in 1946–7 explains the apparent anomaly in this table.

The samples of 582 *G. aculeatus* from Windermere and 27 from Easdale were analysed in the same manner as the monthly samples from the Birket, and the mean lengths in November and June respectively of each year group are shown in Fig. 2; full details of both samples are given in Table 5. It will be seen that while length and growth rate in Windermere are similar to those found for the Birket the growth in Easdale is much faster. The large size of the Easdale fish is therefore a reflexion of a higher growth rate, and not of a longer span of life.

Heuts (1947*b*) has shown that fish of race *A* are generally smaller than fish of race *B*, and this appears to be confirmed by the maximum sizes of populations of these two races recorded in the literature. The sizes of the two largest race *A* fish caught in Windermere and the Birket were 53 and 73 mm. respectively, while Bock (1928) and Craig-Bennett (1931) record 6·0 and 5·5 cm. as the maximum size of fish in their race *A* populations. The largest fish of race *B* recorded by Heuts (1947*a*) was about 79 mm. long (71 mm. to base of tail), Wunder (1930) and Leiner (1931) recorded fish of 70 mm. and about 86 mm. (78 mm. to base of tail) respectively. Bertin records no fish longer than 90 mm. The largest fish from Easdale was 96 mm. It seems that both the Birket and Easdale populations consist of fish which are large examples of their respective races. It is probable that all populations of *G. aculeatus* have a maximum life span of not more than $3\frac{1}{2}$ years, and that differences in growth rate alone account for differences in mean and maximum size of fish in different populations.

This assessment of maximum life span is in close agreement with the work of Bock (1928), Wunder (1930) and Leiner (1930, 1931, 1934), who worked on fish kept in aquaria. This agreement with observations made on captive fish strongly supports the validity of otolith readings when applied to the study of age and growth of sticklebacks.

2. *Pygosteus pungitius*

Table 6 (p. 66) shows the monthly mean lengths of the year groups of *P. pungitius* as determined by otolith readings, taken in the Birket between June 1947 and June 1948. No fish were caught in December and January; the reason for this has been discussed on p. 61. Table 7 and Fig. 3 have been calculated from the data in the same way as for *Gasterosteus aculeatus*.

As for *G. aculeatus*, 1947–8 appears to have been a better year for growth of first-year fish than 1946–7, although this is somewhat obscured by the numerically smaller samples of *Pygosteus pungitius*. Comparison of Figs. 2 and 3 shows that in the first year growth is more rapid in this species than it is in *Gasterosteus aculeatus*, but that in later years the growth rate is slower. The overlap in size of different year groups is seen to be even greater than in *G. aculeatus*, probably as a result of the very slow growth after the first year. It appears that *Pygosteus pungitius*, like *Gasterosteus aculeatus*, lives for about $3\frac{1}{2}$ years, that growth is very rapid during the first year and that in later years little growth occurs.

The fall in the mean size of second-year fish between the June and September quarters shown in Fig. 3 and Table 7 may be explained in the same way as the similar fall in mean size shown by *G. aculeatus*. Owing to the small number of fish in their fourth year it is not possible to state whether the life span of the larger *Pygosteus pungitius* is less than that of the smaller fish.

Relatively few first-year fish were taken, and no very small fish were caught, probably because this species spawns in weed beds in which seine netting is difficult. Apparently the young fish do not move into the open water until they are about 15 mm. long.

No evidence was obtained of autumn breeding as was recorded for fish kept in aquaria by Leiner (1934). The smallest fish caught in the early spring was 33 mm. long, whereas similar fish taken by Leiner were about 27 mm. (24 mm. without the tail). It would seem that Leiner's fish, which were only 6 mm. smaller than spring-caught fish from the Birket, may have been at least 1 year old and not the product of autumn spawning as he suggests, especially as he has pointed out that individual length variation is great. Leiner's observations on aquaria-bred fish show that *P. pungitius* grows more rapidly in the first year of life than *Gasterosteus aculeatus*, which agrees with our observations on a wild population.

The population of *Pygosteus pungitius* in the Birket consists of fairly small fish. The largest recorded was 55 mm. long, whereas Leiner (1934) records a fish of about 85 mm. (7·6 cm. without the tail), and Bertin (1925) implies that the species may grow to a length of 8 cm. Blegvad (1917), however, found no specimens longer than 5 cm. in Danish brackish waters. Without the specimens it is impossible to state whether such large fish are older than $3\frac{1}{2}$ years, but it seems probable that as with *Gasterosteus aculeatus* differences in mean and maximum length in various populations are due to varying growth rates and not to differences in length of life.

3. *Spinachia vulgaris*

Several authors, including Leiner (1934) who knew that both *Gasterosteus aculeatus* and *Pygosteus pungitius* live for 2 or 3 years, state that *Spinachia vulgaris* is an annual fish (p. 60). It was therefore thought that examination of otoliths of this species might substantiate the value of otolith readings for age determination of Gasterosteidae.

Five specimens of *S. vulgaris*, ranging from 107 to 117 mm. in length, were obtained from the sea near

Table 7. *The mean quarterly length of* Pygosteus pungitius *from the Birket throughout the maximum life-span of a fish*

Year of life	Quarter	No. of fish examined	Extreme lengths (mm.) Min.	Max.	Mean length (mm.)
1	May–July	26	15	32	22·4 ± 0·85
	Aug.–Oct.	165	14	39	29·3 ± 0·39
	Nov.–Jan.	3	33	37	34·7 ± 0·39
	Feb.–Apr.	54	28	46	37·1 ± 0·61
2	May–July	30	33	48	40·0 ± 0·68
	Aug.–Oct.	109	29	47	35·3 ± 0·32
	Nov.–Jan.	4	36	44	40·0 ± 1·82
	Feb.–Apr.	109	32	48	41·1 ± 0·32
3	May–July	48	33	50	41·7 ± 0·62
	Aug.–Oct.	21	32	49	39·4 ± 0·80
	Nov.–Jan.	1	.	.	40·0
	Feb.–Apr.	45	34	53	46·4 ± 0·74
4	May–July	19	36	55	45·0 ± 1·28
	Aug.–Oct.	1	.	.	38·0

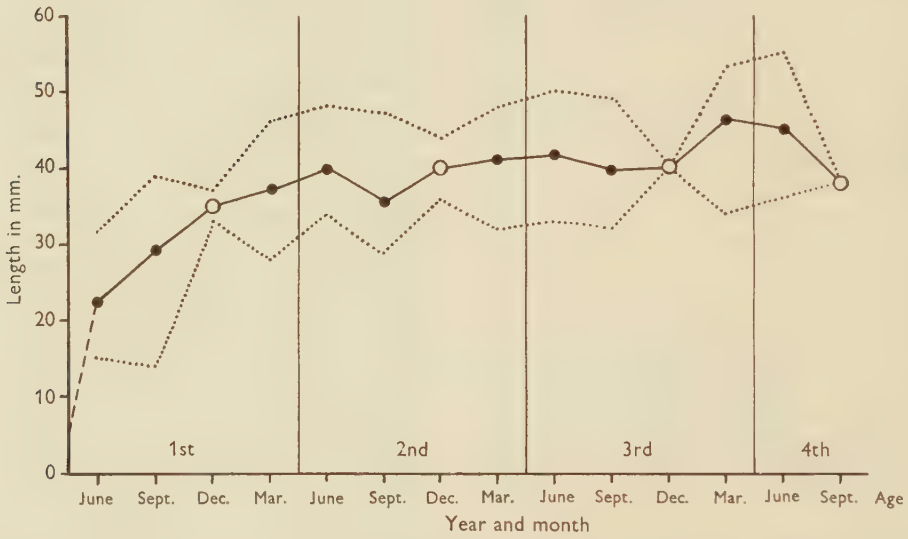

Fig. 3. Average length in each quarter of 635 *Pygosteus pungitius* from the Birket. The dotted lines represent the maximum and minimum lengths, and the vertical lines denote the approximate times of breeding. Open circles represent averages based on fewer than 10 fish.

Great Cumbrae, in December 1948. The sagittae of all were removed and treated in the same manner as otoliths from the other species. No rings were visible in these otoliths, which were uniformly opaque. The opacity was not, however, sufficiently dense to obscure any rings that might have been present.

It seems therefore, that here also, age as determined by otolith readings is in agreement with the findings of previous workers. But it is interesting to note that all specimens of *Gasterosteus aculeatus* and *Pygosteus pungitius* taken during December show one ring. *Spinachia vulgaris* breeds in early summer (Petersen, 1893) so the five fish examined must have been at least 6 or 7 months old, and must have lived through the season June–July, during which the other species lay down the transparent ring in the otolith. This could have some connexion with the suggestion, quoted by Hartley (1947), that annular structures in the hard parts of fishes are spawning marks which, being produced even in immature fish, reflect an

innate physiological rhythm. In a species like *Spinachia vulgaris* which apparently only spawns once, no such rhythm would be established. As, however, the S ring in other stickleback otoliths is definitely laid down *after* the breeding season, and appears in fish which hatched only a few weeks previously, the connexion between spawning and ring formation seems doubtful.

H. AGE AT MATURITY OF *GASTEROSTEUS ACULEATUS* AND *PYGOSTEUS PUNGITIUS*

In view of conflicting statements in the literature (p. 60) regarding the age and size of sticklebacks at maturity, a sample of fish was obtained from the Birket in March 1948, just before the breeding season. The gonads were removed from 90 *Gasterosteus aculeatus* and 90 *Pygosteus pungitius* and fixed in Bouin's solution. Sections were cut and stained in Ehrlich's haemotoxylin and eosin.

Spermatogenesis and oogenesis in *Gasterosteus aculeatus* have been described by Craig-Bennett (1931). In the fish examined all testes showing active cell division were regarded as maturing. The presence of sperm in the testis was associated with an increase in the size of the crypts and a thinning of the crypt tunicae similar to that described in the testes of salmon parr by Jones (1940). Testes showing no signs of spermatogenesis were regarded as immature.

All ovaries showing well-developed oocytes were regarded as maturing, but one female *Gasterosteus aculeatus* in her third year had a large ovary with thick and apparently collapsed walls, and no trace of eggs; it is possible that she was already spent. Ovaries which showed no sign of oogenesis were regarded as immature.

Macroscopically the maturing testes showed varying amounts of black pigmentation and the maturing ovaries were of a large size.

Table 8 shows the age and maximum and minimum lengths of the mature and immature fish of the three age groups present. Most fish were found to be mature, and all but one of the immature fish, a 36 mm. male *Pygosteus pungitius* in his second year, were fish in their first year. It can be stated, therefore, that most fish mature in their first year, and that nearly all spawn again in later years.

This disagrees with the statement of Wunder (1930) that yearling *Gasterosteus aculeatus* do not spawn, and with Craig-Bennett (1931) who found no mature male *G. aculeatus* smaller than 45 mm. long. It agrees, however, with Leiner (1930, 1931, 1934), who maintains that both species spawn in their first year. It is pointed out that Leiner and Wunder worked on sticklebacks from the same region.

Table 8. *Age, state of maturity and length (mm.) of* 90 Gasterosteus aculeatus *and* 90 Pygosteus pungitius *from the Birket, March* 1948

One female *Gasterosteus aculeatus* of 62 mm. was spent.

			Gasterosteus aculeatus			*Pygosteus pungitius*		
Year group	Sex	Gonad condition	No.	Min. length	Max. length	No.	Min. length	Max. length
1st	♂	Immature	2	31	44	3	33	38
		Mature	20	28	48	5	36	42
	♀	Immature	0	.	.	1	36	.
		Mature	25	28	47	13	34	46
2nd	♂	Immature	0	.	.	1	38	.
		Mature	10	39	54	25	32	45
	♀	Immature	0	.	.	0	.	.
		Mature	16	37	54	21	36	48
3rd	♂	Immature	0	.	.	0	.	.
		Mature	9	50	68	7	34	48
	♀	Immature	0	.	.	0	.	.
		Mature	8	50	73	14	36	55

I. ACKNOWLEDGEMENTS

We are particularly indebted to Dr H. D. Slack who discovered the large *Gasterosteus aculeatus* in Easdale Quarry, and obtained the sample for us. We are also indebted to the Freshwater Biological Association who sent us the large sample from Windermere, and to the Scottish Marine Biological Association, Millport, who sent us the *Spinachia vulgaris*. We are grateful also to Prof. J. H. Orton, F.R.S. and Mr Charles Elton who kindly read the manuscript and made many helpful suggestions, and to Mr P. H. Leslie who checked the statistical data, and advised us on its presentation.

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J. SUMMARY

1. The literature on the age and growth of sticklebacks and on the use of otoliths in determination of the age of fishes is reviewed.

2. Techniques for removal, treatment and interpretation of the otoliths of sticklebacks are described.

3. It is shown that in *Gasterosteus aculeatus* and *Pygosteus pungitius* a transparent ring is laid down in the otolith in June or July, followed by an opaque zone laid down between July and the following June. In some otoliths the opaque zone is not visible until September.

4. These two species live for a maximum of under $3\frac{1}{2}$ years, most of them becoming sexually mature during their first year of life.

5. Both species grow rapidly during their first year, *P. pungitius* growing more rapidly than *Gasterosteus aculeatus*. After the first year the rate of growth falls, and growth seems almost to stop in *Pygosteus pungitius*. This results in considerable overlap in size of the different year groups.

6. Variations in mean and maximum size in different populations of *Gasterosteus aculeatus* are shown to be due to different growth rates and not to differences in span of life. It is suggested that the same applies to *Pygosteus pungitius*.

7. *Spinachia vulgaris* is shown to form no transparent rings in the otolith. This supports statements by several workers that it is an annual fish.

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REVIEWS

A FUNDAMENTAL TREATISE ON ANIMAL ECOLOGY

W. C. Allee, Alfred E. Emerson, Orlando Park, Thomas Park & Karl P. Schmidt (1949). *Principles of animal ecology.* 837 pp., 263 text-figures and photographs. W. B. Saunders Company, Philadelphia and London (address in latter: 7 Grape Street, New Oxford Street, W.C. 2). Price $14.00.

Ecological research has been growing in so many directions at once that even its own practitioners must sometimes find it hard to know who is an ecologist and who is not, and just where the subject stands among the other sciences. The general books on animal ecology published within the last thirty or forty years illustrate this variety. Some have been full of facts with hardly any principles; others assay the statement of principles with concrete examples from nature and from experiment, or drift into purely mathematical treatment. Others, less general, deal with such particular branches of the world ecosystem as soil, lakes, oceans or parasites. This is quite a natural stage in the development of a new science, which presumably will try some day to give a consistent account of the living populations of the whole world and their environments that combines factual detail with the sort of algebraic generalization attempted on this scale hitherto only by the late Alfred Lotka.

The authors of the present treatise have seen that the subject is now at a stage of adolescence in which a careful and intelligent appraisal of its achievements and trends may greatly aid its proper development to maturity. Such an enormous task needed a group of people, and it is very fortunate for us that the long tradition of excellent ecological study in Illinois has brought together just such a group of men, with interests and specialized knowledge ranging over and far beyond the conventional field of animal ecology, into physiology, behaviour and evolution. Four of the authors are in the University of Chicago; the other, Orlando Park, is at North-western University. Among famous earlier workers in this region are S. A. Forbes and Victor Shelford.

It is probably a very good thing that ecology should now be examined from a number of angles, lest its important relationships with physiology and behaviour should become obscured by the developing specialisms of those subjects, and by the present engrossment of many ecologists with the purely number relations of animals. For all their position at the core of animal ecology thinking, population data cannot stand alone; they need relating to physiology and behaviour. Any reader of this book who considers that the sedimentary strata of ecology in it have received too many igneous intrusions of physiology or genetics, should bear in mind that his own limitation to purely ecological statements is only necessitated by lack of training in other fields, or by the apparent immensity of opportunities at the ecological or natural history level of fact-gathering. Any good opportunity to bridge such gaps between 'disciplines' should be grasped and may be unexpectedly productive.

Francis Bacon wrote that 'Some Bookes are to be Tasted, Others to be Swallowed, and Some Few to be Chewed and Digested'. This book belongs to the last class. It is by far the most important general treatise on the subject that has ever been published, and one which should, but for its prohibitive dollar price, be in every ecologist's library (whether he be a botanist, zoologist or general naturalist). To any serious working ecologist, and above all to the teacher of the subject, it is above price. The amount of sheer hard reading and analytical thought and writing that have gone into its making fills one with admiration and respect. Nevertheless, it is not exactly an easy work to chew or digest (it has taken me several months, and rumination is still in full swing), perhaps partly because West Europeans have rather different linguistic digestive enzymes from those of the American-trained academic man, who can quickly assimilate and probably expects and demands this standard of solidity. We have to be prepared for an insistence on philosophical definition of terms and concepts which makes the average empirical British ecologist feel rather as if he were having all his familiar old clothing removed by stages for cleaning and pressing. But the interested reader will soon get used to a style that is deliberate and unhurried without being senatorial, and is certainly not episcopal. It has a good many long words like disoperation, protocooperation, homeostasis, contra-indication, meaningful, orientation (of ecologists and ants) and coaction; long phrases like 'the space-time community lattice'; and long sentences that insist on covering every inch of the ground. This is the only general criticism one can make of this extremely valuable treatise: that one has to give some extra attention to extracting the simple meaning from a text already very large and full of necessarily complex ideas. Perhaps one of the authors will, in a fit of summer holiday indiscipline, write quite a short version of this great book, without giving the same attention to qualifying precision of definition, and publish it both in America and Europe, so that every young ecologist can be sure of acquiring more readily the fine intellectual framework of ecological ideas that the larger book contains.

Anyone who takes the trouble to master this great treatise will find himself as well educated in animal ecology as anyone can be from a book. The person most likely to benefit from the experience is the ecologist who has already learned the methods and problems of some part of the subject in the hard way of field work and experiment. I can hardly believe that anyone who really took in the range and depth of what is put into this book could remain narrow-minded.

The general plan of the book runs on the following lines: introductory matter, history of the subject, the environment (mostly from the physical point of view), the properties of populations, community organization (nutritional, temporal and spatial), evolution, bibliography on the grand scale, and a fine index.

After an interesting quotation from Haeckel, 1870, who seems to have understood the point of ecological studies much better than is usually supposed, and a Preface in which the responsibility for authorship is explained, there is a twelve-page Introduction of a general nature. It is more of a discussion-essay than a summary of the book, and I think it is designed more to stimulate thought on certain ideas implicit in the book than to set out any formal position. It discusses, among other things, the place of physiological studies in ecology; drawing a rough line between physiology as a subject dealing mainly with individuals, and ecology as one that handles populations, concerned primarily either of single or of mixed species. Referring to the difficulties of field study in ecology it is remarked that 'The essential impatience of observers is one of the dominant reasons for the growth of experimentation in ecology; but great patience is required for any adequate long-term program of experimentation, the ramifications of which may seem endless'. I think this chapter would be especially valuable to the philosophical non-ecologist or interested student who wishes to know what takes place inside the minds of ecologists. It is stimulating.

The historical sections about the growth of ecology up to 1900, and in the four following decades, take us from the time of Empedocles up to 1942. The sketch of the earlier centuries is rather selective. I should have thought Vergil's *Georgics* worthy of a place in the story. British readers will find the book by L. C. Miall (1912), *The early naturalists*, which is not referred to here, a useful additional guide to the trends in European natural history and its small content of ecology. There are certain milestones that would be worth notice, such as the notions of Da Acosta (*c.* 1540–1600) on the zoogeography of America; and the growing knowledge of altitudinal zones by l'Obel, Linnaeus, Ramond and Humboldt. The omission of Humboldt's *Cosmos* and his *Travels in South America* from the bibliography is rather hard to understand. He always seemed to me to be one of the earliest scientists to understand that the world could be contemplated as one ecosystem. It is true that his works are mostly very tedious to wade through; yet Darwin gained much inspiration from the *Travels*.

One feels that the Classical and Mediaeval ages had little more ecological knowledge than any well-educated person might acquire by using his observation and common sense out of doors. Later, it was an accident of scientific history that the proper growth of ecological field studies was delayed during the nineteenth century because biologists concentrated so much upon collecting and bringing indoors fragments of the plant and animal community.

It is fair to say at this point that the comparative completeness of the treatise makes it rather easy to notice and point out single omissions, which are inevitable, since no group of men can cover the whole of ecology in detail, and in any case the selection of examples for a publication has to be pretty severe. There are, in general, very few important gaps in the jigsaw puzzle the authors have fitted together, and it will be as well if I emphasize the enormous range of literature and facts that are canvassed in more or less detail. A good many names are brought into the historical account that are not usually thought of in an ecological connexion, such as that of Farr, with his epidemiological law; and Quetelet (an early nineteenth-century Belgian demographer). We learn that Malthus devised the phrase 'struggle for existence'; and that Verhulst, whose logistic curve was resurrected by Pearl, did in fact fit his equation to some West European human populations. The originality of Semper's ecological outlook is brought out to an extent one had not at all realized.

A good deal of the progress reported in biology during the nineteenth century seems to fall rather outside the province of ecology, being physiological in content. For example, the inability of a snake to poison itself by its own bite seems to fall in such a category. The chief thing that the pre-1900 survey brings out is the extreme paucity of real ecological thinking. The facts were being slowly accumulated, like underground roots of the plant that was to grow up in the present century. In my opinion, animal ecology hardly existed as a coherent general subject or attitude in the nineteenth century, except in human demology and within the particular field of limnology, and even here the animal community had hardly been analysed at all except as total lists of species in particular communities like plankton. There were many first-class men doing field work and some interesting pioneer thinkers on the subject. All these paved a path that was not to be regularly trodden until after 1920. In this connexion it is noted that 'modern community studies have been mainly stimulated by Warming's findings rather than by those of his zoological predecessors, Edward Forbes, Verrill, Möbius and S. A. Forbes'.

In the earlier period, and still to a considerable extent, the ideas and methods of ecology have developed along separate tracts that should form one subject, but have been isolated by tradition or economic bias. So there have been animal sociology, limnology, oceanography, fisheries, economic entomology (especially the part dealing with counter-pests and fluctuations) and disease vectors, as well as natural history. These sectional trends are discussed in a very interesting manner, but it must be obvious that we cannot hope to establish any simple phylogeny of ecological concepts. But the present account, and more particularly the fuller sections about history since 1900, should become part of the cultural currency of every ecologist.

The period 1900–20 saw a big move forward in animal community concepts, and in the quantitative measurements of certain ecosystems—notably lakes. There was Petersen's remarkably original study of the Danish sea-bottom ecosystem, to which I do not think even the tribute given in the book gives full justice. Shelford, and Adams, translated some of the plant ecological ideas into animal terms, though without yet developing the population concept.

The history of the next 20 years is well described, though from most readers' familiarity with it, it need not be discussed here at length. The foundation of the Ecological Society of America in 1916 is mentioned. Though the book states that it has emphasized American examples in ecological history, owing to accessibility of the knowledge, one might note that the British Ecological Society was founded in 1913, and refer readers in this country to the interesting account of its origin and the work of pioneer British ecologists, published by Tansley in the *Journal of Ecology*, 1947, 35: 130–7.

I now come to a consideration of the main bipolarity

shown in the structure of the book, indeed of ecology generally. This is the balance of studies resulting from a certain methodological conflict. On the one hand the analysis of simple population situations, by experiment or by mathematical deduction, is an accurate and to certain minds satisfying approach towards eventual integration at high levels; and set opposite to this, the instinct of the natural history-minded ecologist is to survey what actually lives in wild communities, with the proportionate difficulties set by multi-species populations set in environmental settings with complex horizontal, vertical and temporal patterns. This bipolarity is well illustrated by the past and present research contributions of two of the authors: Orlando Park, on community structure and temporal changes in activity and of community facies; and Thomas Park, on the exact or probable results of maintaining one, or at most three, species in various states of interaction in highly simplified (but still not simple) laboratory environments.

First of all, however, something should be said about the large and excellent section (190 pp.) called 'Analysis of the environment'. In this almost every feature likely to concern the ecologist (and a few, like earthquakes, that are not so often likely to do so) are described in an accurate and critical manner. It starts with a discussion of the 'fitness of the environment' (which has recently acquired a renewed interest, since we have been told by astronomers of the probable abundance of similar worlds in other parts of the galactic system, or in further nebulae: it is even conceivable now that some other planet has an ecological society a million years old). In this part I would have included A. H. Church's brilliantly suggestive monograph on *The building of an autotrophic flagellate*', which is not referred to. There follow chapters dealing with radiation in general; heat (here we learn that 'a lake is a rather neat environmental unit'!); light, gravity, pressure and sound; currents of air and water, surfaces of water and land; certain physical and chemical factors like viscosity and osmosis; water in its various forms; gases; dissolved salts, regarded as limiting factors; climograph or combined factor studies; and the ecological relations of soil. The whole treatment here seems to be careful and full without attempting to be encyclopaedic, but as much of it is outside my competence to criticize, I will leave it with a respectful and grateful bow.

The next chapter, 'Biotic factors in relation to individuals', seems to overlap in principle some of the later part on community structure. In fact, it seems to be a bit adrift within the general plan of the book. It deals professedly with 'autecology' (which it is carefully explained, is *not* the ecology of single species populations, but of individuals; cf. p. 48 in the History section where the intentions of Schröter & Kirchner (1902) are explained). The account of shelter created by plants, with consequent microclimatic modifications, is useful, but it is a bit hard to see why 'plant cover' comprises only the individual plant rather than vegetation in general, which is population. Other subjects include symbiosis, commensalism, parasitism, feeding adaptations and food as a limiting factor. Among feeding adaptations pollination is discussed in general terms. The survey of these subjects is interesting, but rather brief and limited in scope.

Undoubtedly for many working ecologists Section III on Populations, which forms the middle part of the book, is one of the most stimulating and important. It begins with a rather markedly formalistic treatment of the general properties of populations, and proceeds through a summary of types of census and counting methods, to deal successively with reproductive capacity and performance, life tables, age distributions, true (intrinsic) natural rates of increase, the logistic curve, and then with various examples of growth forms, or rather actual case histories of growing or fluctuating populations, derived from experiments and some field records. The account of methods of analysis is first-rate in calibre, and gives in a simple and comprehensible form some of the leading ideas from human demology, as well as many instances of experimental animal populations. This part of the section finishes up with the different factors that may affect population rates, considered broadly under physical (mainly non-density-dependent) and biotic (mainly density-dependent) categories. The physical examples are rather a patchwork, and it is under the biotic ones (which comprise such major influences as food, competitors, enemies and parasites) that the analysis reaches its best level. Tacked on to this part of the argument are interesting summaries of the overfishing problem and of some field studies by Barber on the cornborer moth.

The discussion of census procedures is done under the headings of total counts (known only from the laboratory, a few very local and rare forms of interest to conservationists, and with some errors, man); total counts of certain life-history stages; registration (a theoretical method, of counting and then recording subsequent additions or departures); sampling (with suitable warnings about the statistical snags); marking live animals; and the use of indices. There is a shrewd remark at the end to the effect that 'The reader will recognize that, while this problem is technically the central one in population research, it is often a difficult one to put into actual, accurate operation. He will recognize also that some of the applications in the literature are inadequate for one reason or another, and that in planning any population venture this whole matter demands prior thoughtful attention'; which is partly a polite way of saying that much of the published census work is no good! The same might be said about most published figures for potential rates of increase of species. When this book was written there were less than half a dozen instances in which the true (or intrinsic) rate of natural increase was correctly known. Since it was published a few more have been worked out. The text explains very clearly the data that are needed in order to calculate such a figure, which is always far less than that reckoned merely from the reproductive potential. When the maximum possible density is considered as well (as in the excellent discussion of the logistic curve and its assumptions) the potential numbers attainable even temporarily by a species appear even more modest.

As regards the logistic curve, the very fair comment is made that 'Despite the criticisms that can be levelled against it, the logistic curve, when not overinterpreted and when used intelligently purely as an empirical record of population growth, is a valuable demographic tool'. A proper appreciation of the place of this equation in population theory seems desirable, since it enters to an important extent (though presumably it is not the only

one that could be used there) into more complicated equations of competition and other interspecies population interactions.

The various special instances of growth histories and fluctuations range from laboratory animals to fur-trade statistics (which, incidentally, are not strictly population curves, but rough indicators of population change), and from diatoms and bees to man. The explanations of competition, predator-prey and host parasite fluctuations are very lucid and valuable, and the ecologist is reminded that he must be mentally aware that any population he studies has a past history which partly explains its density and structure at the time it is under investigation. One is, in fact, never studying an average situation.

It is not made clear that the experimental oscillations induced by Gause in *Paramecium*/yeast populations were only kept going by additions of individuals at intervals. No one, so far as I know, has ever maintained oscillating two-species populations in the laboratory for more than one or two cycles without subsidy from without. This situation has been discussed by Nicholson theoretically, and may, indeed, sometimes actually obtain also in nature.

The final two chapters under Population deal with animal aggregations and with insect societies. Both are good summaries, and the insect one has some excellent photographs. Animal aggregations are seen as a stage in the evolution of more elaborate societal groupings. Such aggregations carry the physiological or other advantages to be gained from a state of slightly or local high density, lying between lower and higher densities that may carry considerable disadvantages.—The idea here is of an 'optimum stage of aggregation'. Although there are a number of thoroughly proved instances where undercrowding brings relative disadvantages for survival, rates of increase and so on, and this does give a reasonable hypothesis to explain the initial unorganized stages of social aggregation, I have never been able to decide how common undercrowding in nature is. Presumably it actually limits or slows down the initial rates of recovery in populations that have reached very low numbers. In certain populations this factor might be just as important currently as the more dim future possibility that the species might reach a social state during evolution. The phenomenon of 'Allee's undercrowding' therefore merits attention, both for its importance in the theory of social evolution and for its effect on fluctuating populations. And, of course, aggregations are themselves of great ecological interest, and to judge from the examples cited, more common in the field than one might have supposed.

A very interesting instance from human populations, cited here, is that of the Mennonite colonies in North America, whose limiting minimum number of families for successful survival of a colony is stated to lie between twenty and fifty. This chapter concludes that 'natural unconscious mutualism is one of the basic principles of biology', and this reminds us that the real extent of competition versus co-operation between species, and between species groups and communities, has still to be explored and understood.

The chapter on insect communities is necessarily very condensed, but is stimulating, and technical terms are at a mercifully low density. Its main purpose is to explain what is known about the degrees of integration in such societies.

The large Section IV on the Community I have found the most difficult to grasp wholly and to appraise, but I think that is mainly because of the extraordinary range of material that exists on the subject, if, as the book does, we include discussion of organismal concepts; stratification vertically and horizontally (which in this country is usually called zoning) in all the major ecosystems; metabolism (meaning here food relationships and community structure in the widest sense); periodic activity rhythms affecting community life by season and by day and night; and ecological succession, climaxes and biomes.

The community is conceived along these lines: 'The major community may be defined as a natural assemblage of organisms which, together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self-sustaining.' Provided we underline the word 'relative', this seems fair enough. It is pointed out, as example, how there is a difference between a comparatively self-sustaining forest system, and the bracket fungus community depending on a particular tree in it.

'Stratification is applied in the broadest meaning of the term, and embraces all objectively delimitable vertical or horizontal layers of organisms, their by-products, or the results of their activities upon the environment.' It is thought of as primarily laid down by the accumulation of succession stages, with changes by reaction within the community, and the development of various minor layers or niches giving variety to the habitats. I would prefer to call it a pattern in three (or four) dimensions, and I suppose that is the same idea contained in the term 'space-time lattice of the community', used in the book. Implicit in the discussion of this concept is the idea of partial integration of segments, layers or minor bits of the community into separately organized affairs. This process, it is recognized, never becomes complete—if it did we should have no migrant birds, no dynamic pattern in major communities, and probably an enormously accelerated production of ecospecies.

From this basis, the account goes on to describe in good summary various gradients and their zonal community types on water and land, ending up with the forest community, in which is included an interesting table comparing some ecological types of animal niche in forests of the five continents.

With the chapter on Metabolism, the pace is faster, and the approach more analytical and less purely descriptive. The circulation of matter and energy is discussed, the chemical and bacterial parts being of special significance to those unfamiliar with the subject: 'Our general conclusion is that bacterial activity is of fundamental importance in the metabolism of all major communities; that these activities are essentially similar in all major communities; and that these processes are carried out by many ecologically equivalent species of bacteria. Ecologists as a group have been more aware of the place of the second key industry, photosynthesis, in the metabolism of communities than they have been of the role played by bacteria.'

Food relations (layers, chains, cycles, etc.) are very succinctly described, but I do not agree that it is a good

change to introduce the term 'food mesh' for 'a taxonomic entity in a food web' (i.e. food cycle, etc.). But it seems a distinct improvement to talk of 'food niche' to distinguish this concept from 'habitat niche'. I was glad to learn that Semper and S. A. Forbes about the eighties of last century had each realized the idea of the pyramid of numbers. (Peter Breughel the Elder drew a wonderful picture of food chains among fish (plus man) in the sixteenth century which probably contains the same idea; and the native fishermen of Lake Albert whose delightful food-chain fishing method has been described by the Worthingtons, put it to some practical use.)

It would seem that the formulation of energy budgets has been carried furthest by limnologists, the work of Juday and his group, and later on of Lindeman, being especially valuable. The diagram of biomass in different producer and consumer layers and of dissolved organic material in Weber Lake, Wisconsin (from Juday's work), is especially striking, as showing the pyramid from basic resources up to fish.

The treatment of seasonal and diel periodic changes in species (and therefore community) activity is extremely good, and covers every aspect of the subject. The sections on succession and biomes follow conventional lines, and are well documented.

Of the section on Ecology and Evolution I shall not say very much, as it deals mainly with subjects outside my competence. It is clearly sound that evolution should be given a place in a modern book on animal ecology. After those on induced mutation, and the relation of fluctuations in numbers (i.e. different densities and dispersion) to the fate of mutations, the chief important parts deal with ecological isolation, natural selection (including some mention of selection pressure and Sewall Wright's exploratory ideas), and 'the evolution of interspecies integration and the ecosystem'. The discussion of the last subject is rather discursive, though full of interesting material, and I feel that it rather missed its opportunity of coming to grips with the very subtle question of whether any large ecosystem can be selected as a whole, in the sense that its integration dynamically is complete enough to make it into a quasi-organism (Tansley's term) with some survival importance on its own merits at that level. I was surprised that Tansley's key essay on the ecosystem ('The use and abuse of vegetational concepts and terms', *J. Ecology*, 1935, 16: 284–307) was not mentioned.

In conclusion, a word about the format of the book. It is strongly bound and weighs a great deal more than is comfortable for carrying on a journey or reading in bed. The type is pleasant, and the text-figures very good indeed—they have mostly been redrawn boldly and clearly from the originals. The photographs are also good, but I suppose it is on their account that the paper is heavy and shiny, with resulting increase in weight. It is not improbable that the book could have been written in about three-quarters of the space, and if it were printed on lighter paper it would certainly be easier to use. There is 'a bibliography to end all bibliographies' of perhaps more than 2500 references, evidently checked with some care. An unusual and useful feature is page references to the places in the text where each publication is mentioned. The index is excellent, and very full.

It is difficult for even an earnest reader to do justice to the enormous amount of material assembled and discussed in this grand book. Any deficiencies in the present review are due to the scale and completeness of the volume, and the impossibility of quickly absorbing in a productive fashion all the ideas and facts presented there. It should provide a resource for ecologists for many years, and whether it is entirely right or wrong in particular ideas and details is probably unimportant, and certainly need not worry the authors, who are to be congratulated on the high level of balanced intelligence with which the book has been done. Somewhere in the *Pilgrim's Progress* one of the actors says: 'Our great want awhile since was harbour and good company, and now I hope we have both.' CHARLES ELTON

THE TECHNOLOGY OF WILDLIFE MANAGEMENT

Reuben Edwin Trippensee (1948). *Wildlife management: upland game and general principles.* 479 pp., numerous text-figures and photographs. The American Forestry Series, New York. Price $5.00.

Aldo Leopold has included game management in the arts,[1] and there is much evidence in Prof. Trippensee's book that an intuitive approach must continue to play an important part. Few recommendations for habitat improvement, for example, can be advocated on a basis of controlled experiment; but, in so far as the advice conforms to sensible practices of land use, this aspect of wildlife management has a higher social and ethical value than the mere production of larger game crops. The last 20 years have seen an enormous growth of wildlife technology. Of Prof. Trippensee's 76 references on deer all but four were written in 1930 or later, and his book will be the first to be consulted by anyone searching through this vast and scattered literature. For in addition to such sources as the *Journal of Wildlife Management* (432 pp. in 1949) and the *Transaction of the North American Wildlife Conference* (635 pp. in 1949) there are 36 State game department periodicals[2] of varying degrees of value and numerous Federal publications, including the Pittman-Robertson Quarterly—of which the issue for July 1949 consisted of 150 pp., outlining current research and other projects.

Before discussing the present book let us sketch in some of the physical and intellectual background to the wildlife picture in America: first, the type and extent of a few administrative problems. *Texas Game and Fish* for August 1949 gives four pages of extracts from the new game and fish laws, which range from opening the squirrel season for two months in Cherokee county to closing it on deer for five years in Limestone county. (There are 254 counties in Texas, including 5935 sq. miles in Brewster county alone, and the laws cover minnows, turtles, quail, peccary and other species.) The Michigan Department of Conservation[3] had a recent budget of over eight and a half million dollars, of which 13–14 % each was spent on law enforcement, game management, fish management (Michigan has one million sportsmen) and on forest fire protection, 10 % on running parks and recreation areas for 12 million visitors, 2·6 % on education. One further illustration: Pennsylvania seeks in part to

protect her game by a bounty system, which during 1949 offered the following rates:[4] $1 for a weasel, $4 for a fox, $5 for a great horned owl or goshawk and half this sum for each of their fledglings. These examples are enough to show the importance of schools of wildlife management in training the men on whose advice these policies should be based.

Next, consider the difficulties of the wildlife technician. His income is derived from sportsmen, some of whose organizations are powerful; but they may have no higher objective than a large kill, nor any sounder notions about providing it than to erect 41,000 miles of fencing to cut down highway mortality of rabbits, or to import stock at a cost of $100,000 for an estimated increase in density of two rabbits per sq. mile.[5] However, even if his work is unobstructed, the technician is dealing with highly complex communities. He is trying to manipulate laws of population dynamics, although their application even to small laboratory populations is as yet imperfectly understood. Finally, much time has to be given to problems such as estimating crippling losses, proportions of geese carrying lead shot or the number of coots per hunter-day. Though each of these questions has its own importance, many are of little scientific interest.

The main distinction between science and technology is generally held to be one of aims and not of method,[6] (though practical demands reduce flexibility and impose special difficulties which academic workers do not always appreciate). To say that science does not profit by discoveries in technology would be as false as to say that technology can advance without a set of empirical scientific laws; but while a technology cannot be judged by the extent of its contribution to science, it may be criticized if it fails to make the best use of scientific principles. The justice of this distinction is illustrated by a passage (not to be taken too literally) from a *Newsletter* of the Wildlife Society, advising students to undertake summer employment:[7] 'The performance of such tasks as harvesting agricultural crops for wildlife usage, opening up stands of timber, planting trees and shrubs, performing stream improvement work, digging postholes and constructing fences, cleaning game bird pens and fish ponds, and mixing and distributing feed, give students good practical experience on what they may be doing after they get their degrees and go permanently to work...and the student may decide that he is better fitted for other than wildlife or fishery work.' We have therefore to consider whether 'Wildlife Management' is likely to be useful to survivors of this tough apprenticeship, which, one might guess, would eliminate those of a primarily intellectual bent. Two questions seem appropriate: how far are existing facts unified and how much guidance is offered in the principles of population control?

A partial answer to the first has already been given, but it is well to emphasize that this task of collation is an essential step and that the author's aim has been achieved 'at least [to] provide starting points'. Further discussion thus applies less to the book itself than to the subject.

The chief difficulty is how to deal with the mass of observations on particular populations under a wide variety of conditions. A general treatment is admittedly difficult, and the author has tended to give a series of reports on techniques and observations and to leave the reader to form his own impressions. An example of the consequent difficulty is provided by the discussion of three studies of deer foods: 'too literal an interpretation of the table is not warranted. Discrepancies exist, and in certain respects the tables are not comparable. However, if these limitations are borne in mind, they should not detract seriously from the over-all impression that the table is meant to portray.' (p. 197). My analysis of this table is given below:

Study	A	B	C	
Total no. foods	7	6	10	Preferred foods
No. common to A, B and C		1 (?)		Preferred foods
No. common to two lists only	1	2	1	Preferred foods
Total no. foods	20	9	20	Readily eaten foods
No. common to A, B and C		1		Readily eaten foods
No. common to two lists only	2	3	3	Readily eaten foods

Although there are a few other points of agreement, the over-all impression is somewhat elusive, and we are left in doubt whether the compilation of further lists is a reasonable objective, and if so how general their use will be.

In contrast to Leopold's *Game Management* the arrangement of the present book is more by species than subjects, and its emphasis upon facts rather than principles. If current views are fairly reflected, a rather undiscriminating faith is shown in the collection of data, with too little consideration of their relative value.

An outsider has the doubtful advantage of being able to form his views with an incomplete knowledge of the many exceptions to them. The following remarks are therefore offered with reservations, but in the belief that Prof. Trippensee wrote his book to assist this sort of generalization. There seem to be three breaks in the chain of effort: the first is a failure to adopt the concepts and working hypotheses of current ecological thought (a situation that may not improve under too vigorous a growth of the practical schools). Then, even with the knowledge already held by the wildlife technician there is a serious gap between his advice and the action of State legislators and executives. Most writers on wildlife conservation quote examples of wasteful policies: artificial propagation, bounty systems and deer control are cases in which the best information and advice may be put to little use. Thirdly, even the wisest laws are of little value if the public has no 'ecological conscience' (a term of Aldo Leopold's).

Several recent books have shown us the seriousness with which Americans regard the conservation issue. Problems of wildlife management are closely bound up with this complex social problem, and indeed the greatest opportunities for progress seem to be at this level rather than at the technological. If this conclusion is correct it suggests that the significance of short-term projects, however competent, is dwarfed by the larger issues—which further suggests, as an ideal, some reorientation of effort. As already shown this will not be easy. The sportsman expects a quick return for his money and might be unsympathetic (to name the mildest of his emotions) towards an investment in fundamental research on populations of yeasts, beetles or mice, or in education in nature conservation.

Remedies against the depletion of a resource are seldom easy and politically possible, and although a solution must be found, much effort will be wasted if the tempo is unduly forced. In population studies, especially of vertebrates, some years may be needed to overcome technical difficulties alone, after which time must often be reckoned in minimum units of a generation or a cycle in numbers of the species. It would be wrong therefore to close this review without a tribute to the success which, in spite of great difficulties, has attended so much of the study and conservation of the American fauna.

DENNIS CHITTY

[1] Leopold, A (1947). 'Game Management.' Encycl. Brit., 3 pp.

[2] Anon. (1949, 1950). Wildlife research news letters, nos. 38, 40. Univ. Wis., Madison. (Quoted by permission.)

[3] Walker, G. A. (1949). Mich. Cons., May–June: 28–30.

[4] Anon. (1949). Pa. Game News, July: 20.

[5] Latham, R. M. (1949). Pa. Game News, Oct.: 12, 19, 24.

[6] Caldin, E. F. (1949). 'The power and limits of science: a philosophical study.' London.

[7] Rutherford, R. M. *et al.* (1947). Wildlife Soc. Newsletter, Jan.: 1–4.

CONSERVATION IN SCOTLAND

Nature Reserves in Scotland. Final Report by the Scottish National Parks Committee and the Scottish Wild Life Conservation Committee. Cmd. 7814. 1949. 34 pp., 1 folding map. H.M. Stationery Office, Edinburgh. Price 1*s.* 3*d.*

The Scottish Wild Life Conservation Committee was less fortunate than its counterpart for England and Wales, which found the spade-work of preliminary selection of nature reserves already done for it by the Nature Reserves Investigation Committee. In consequence its final report has been delayed till two and a half years after the single complete report of the Wild Life Conservation Special Committee (England and Wales), which was published in July 1947 as Cmd. 7122, and was reviewed in this *Journal* (vol. 17, pp. 81–2) along with the first report of the Scottish Committee (Cmd. 7235), which dealt solely with matters of organization and administration. The present report is therefore comparable with the report on *National Nature Reserves and Conservation Areas in England and Wales*, issued by the Nature Reserves Investigation Committee for England and Wales in December 1945 as well as with the relevant parts of Cmd. 7122, which were in fact substantially based on the N.R.I.C. report.

The present report recommends the creation of four national park reserves, twenty-four national nature reserves, twenty-two nature conservation areas, and one 'special case', a conservation area of nearly half a million acres in north-west Sutherland. National park reserves are defined as 'selected areas within the Parks . . . where the larger mammals and birds may breed in safety, and where the survival of the rarer plants may be assured'. These reserves would be controlled either by the Scottish National Parks Commission (not yet even in a bill before Parliament) or by the Scottish Committee of the Nature Conservancy, which was set up earlier in 1949. National nature reserves are equivalent to those recommended for England and Wales in Cmd. 7122, and nature conservation areas are equivalent to the 'scientific areas' proposed in that report. It is unfortunate that the nomenclature could not have been kept uniform, but it must be admitted that the Scottish term is better than the English.

Attention naturally focuses on the two dozen national nature reserves, and here the southerner is at once struck by the relative uniformity among the areas chosen for preservation in Scotland, compared with England and Wales. Indeed, one is almost tempted to suggest that a single English county, such as Kent or Norfolk or Devon, could show more richness and variety of habitats than the whole of Scotland. Small islands will naturally bulk large in any list of Scottish habitats, but here are seven nature reserves consisting of marine and two of fresh-water islands, while marine islands form important parts of three other reserves. Again, there are no fewer than seven coastal or estuarine reserves, apart from the islands, which leaves, as will be seen, only eight for the whole range of inland terrestrial habitats in Scotland. Only three reserves appear to be primarily designated as such for their woodland, compared with twenty-four out of the seventy-three reserves proposed for England and Wales. This is a terrible indictment of man's devastation of a country which was once predominantly wooded, but it also reflects the much greater uniformity of the natural scene north of the Cheviots. In Scotland there is none of the rich diversity introduced into England by the successive belts of the Trias, the Oolite and the Eocene beds crossing the country from south-west to north-east. Nor do there appear to be so many of those small areas, so attractive to the ecologist, where this richness and diversity appears in an area so small that the eye can compass it, as in Purbeck and the Isle of Wight.

This is not to say, of course, that there is not a vast amount in Scotland that is very well worth preserving, including an arctic-alpine flora and fauna much richer and more varied than anything that England and Wales can show. The student of sea birds and wildfowl, also, will be grateful to the Committee for the care with which their choicest natural communities have been selected. There can be few people living with a wide enough knowledge of the Scottish countryside to be able to judge truly whether or not the Committee's selection of reserves and conservation areas is the best possible, but the report bears the stamp of the care brought to their task by the distinguished naturalists who have given so much of their time to serving the community in this important way. All ecologists visiting Scotland are in their debt for providing such a compendious guide to the areas which they ought to see, and if the Nature Conservancy succeeds in preserving for future generations of naturalists even half these areas, the Committee may feel well satisfied.

R. S. R. FITTER

URBAN BIRD COMMUNITIES

R. S. R. Fitter (1949). *London's birds.* 256 pp., 26 half-tone illustrations, 2 end-paper maps. Collins, 14 St James's Place, London, S. W. 1. Price 10*s.* 6*d.*

This is a more intensive survey of part of the ground already covered by the author in *London's Natural History* (see review in this *Journal*, 16: 95–6). The area now under consideration is smaller, consisting only of the Administrative County of London, and attention is confined to birds.

The account is pleasantly written, carefully documented, and treated by habitats, which makes it easier to read than if it had been treated by species. The discussions revolve round certain major topics, which are of considerable biological interest, and which focus on the adaptability of certain species (often unexpected ones) in settling into such an 'unnatural' environment. The most illuminating changes have occurred during the last hundred years or so, which have seen the final driving out of many species that hung on while there were still open spaces and fields, and the incursion of such species as carrion crows, wood pigeons, tawny owls and (in winter) starlings, gulls and many kinds of duck. The interesting question, neglected by most authors, of London's semi-domestic pigeons is treated at some length.

A useful biographical Appendix is given on various authors who have written about London's birds, and there is a full index.

H. N. SOUTHERN

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Several papers omitted in the last few years are being noticed in this and following issues. Papers in the *Journal of Animal Ecology* itself are not dealt with. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, Department of Zoological Field Studies, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by H. F. Barnes, E. M. Cawkell, P. G. Corbin, G. I. Crawford, A. E. Ellis, U. M. Grigg, C. Matheson, E. Nelmes, H. G. Vevers and G. Watt; checking by B. M. Hobby, abstracting and editing by R. S. R. Fitter.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Cole, H. A. & Jones, E. W. Knight (1949). 'The setting behaviour of larvae of the European flat oyster *Ostrea edulis* L., and its influence on methods of cultivation and spat collection.' Fish. Invest. (2) 17 (3): 1–39.

Data from work in experimental tanks. Gregariousness of the larvae and a preference for settling on fouled surfaces are newly brought to light. The larval behaviour of the two genera *Gryphaea* (oviparous) and *Ostrea* (larviparous) is compared.

Comfort, A. (1946). '*Patella vulgata* L.: relation of habit to form.' J. Conch. 22: 216–17.

Effects of the habitat on shell form in the limpet.

Fraser, J. H. (1949). 'Distribution of Thaliacea (salps and doliolids) in Scottish waters, 1920 to 1939.' Scot. Home Dep., Fish. Div. Sci. Invest. No. 1: 1–44. H.M. Stationery Office, Edinburgh. Price 2*s*.

These plankton 'indicator' species are brought in by the Atlantic current and thrive only in warmer waters. There appears to be an annual variation in the origin and quality of Atlantic waters and an inverse relationship between the influxes in Scottish areas and those through the English Channel.

McMillan, N. F. (1947). 'The ecology of *Limapontia capitata* (Müller).' J. Conch. 22: 277–85.

Account of the life history, food, habitat, enemies and resistance to low salinities of a salt-marsh gastropod.

McMillan, N. F. (1948). 'Possible biological races in *Hydrobia ulvae*(Pennant) and their varying resistance to lowered salinity.' J. Conch. 23: 14–16.

The resistance of a semi-marine gastropod to low salinity shows considerable variation in different localities, indicating the existence of physiological races.

McMillan, N. F. (1948). 'The resistance of *Hydrobia ventrosa* (Montagu) to low salinities.' J. Conch. 23: 16.

Experiments on the toleration of lowered salinity by a brackish water gastropod.

Pyefinch, K. A. & Downing, F. S. (1949). 'Notes on the general biology of *Tubularia larynx* Ellis and Solander.' J. Mar. Biol. Ass. U.K. 28: 21–43.

Particular attention paid to settlement of the larvae, and to the factors affecting the growth and development of the colony.

Wilson, D. P. (1949). 'Notes from the Plymouth aquarium.' J. Mar. Biol. Ass. U.K. 28: 345–351.

Aquarium observations on a disease of *Adamsia palliata*; longevity of sabellids; learning in *Palinurus*; regeneration of arms in *Marthasterios* and of fins in *Trigla hirundo* and *Mugil chelo*; partial burying of *Trigla hirundo*; shoaling of *Gobius flavescens*; guarding of eggs by *Blennius gattorugine*.

(*b*) Fresh water

Anon. (1949). 'Bryneuryn Weir in 1847.' Proc. Llandudno, Colwyn Bay and District Field Club, 20: 27–9.

Brief notes on the quantities, species and prices of fish taken at Bryneuryn Weir, Llandrillo-yn-Rhos, Denbighshire, between 1847 and 1850.

Bloomer, H. H. (1946). 'The seasonal production of spermatozoa and other notes on the biology of *Anodonta cygnea* (L.).' Proc. Malacol. Soc. Lond. 27: 62–8.

Analysis of stage of development of sperm morulae and spermatozoa of 63 swan (*Anodonta cygnea*) between January and August 1945.

Garnett, M. (1946). 'Winter birds on Windermere: a retrospect together with a list of the water-fowl, waders and gulls of the lake.' Trans. Carlisle Nat. Hist. Soc. 7: 49–70.

Contains much information about the feeding and roosting habits of the birds of this ten-mile-long lake.

Johnston, T. L. (1946). 'The grey lag-goose in Lakeland.' Trans. Carlisle Nat. Hist. Soc. 7: 75–87.

Describes the increase and spread of *Anser anser* in the area, with notes on changes in habitat and feeding habits.

Jones, J. W. (1949). 'Studies of the scales of young salmon *Salmo salar* L. (juv.).' Fish. Invest. (1) 5 (1): 1–23.

A study of 3000 parr and smolts from British rivers relates growth rings of scales to age, rate of growth, feeding, spawning and the possible identification of fish of a particular river. Data of the proportions of sexes are given.

Kuiper, J. G. J. (1949). '*Pisidium pseudosphaerium* Favre in England.' J. Conch. 23: 27–32.

Description of a freshwater bivalve new to British Isles, with notes on habitat.

Longfield, C. (1949). 'The dragonflies (Odonata) of the London Area.' Lond. Nat. for 1948, 28: 80–98.

The first part of the paper contains an account of changes in the collecting grounds and the general distribution of dragonflies within the area since the early nineteenth century, with a list of the 36 species recorded from it, indicating their present vice-comital distribution; 32 species are still represented, and in general pond dwellers have increased and bog, marsh and river species lost ground. The second part comprises details of localities, habitat preferences, abundance, breeding records and seasonal appearance for each species.

McMillan, N. F. (1947). 'Mollusca of a temporary pond.' J. Conch. 22: 268.

Description of a pond which dries up in summer and its molluscan fauna.

Perry, R. (1949). 'Field notes on some Badenoch dragonflies.' Scot. Nat. 61: 36–49.

Includes notes on the habitats of eight species.

Rooke, K. B. (1949). 'Radipole Lake, Weymouth, as a Bird Sanctuary.' Proc. Dorset Nat. Hist. and Arch. Soc. for 1948, 70: 134–42.

The history of the sanctuary, which is threatened by 'development', is given together with an account of the birds to be found there. This list contains 109 species, of which 35 are decidedly rare. An appendix gives the number of wild duck seen on the lakes of Radipole, Crichel and Sherborne during the year.

Stratton, L. W. (1946). 'Erosion of *Lymnaea stagnalis*.' J. Conch. 22: 208–14.

Effects of environmental factors on the shell of a pond-snail.

Warwick, T. (1946). 'The inheritance of the keel in *Potamopyrgus jenkinsi* (Smith).' J. Conch. 22: 200–1.

Experiments on effect of environmental factors in inducing shell variation.

Warwick, T. (1947). 'Molluscs in thermal pools at Matlock Bath.' J. Conch. 22: 273.

Four species of freshwater snail inhabiting water of constant temperature and composition.

(*c*) Land

Baker, H. G. (1949). 'Differential susceptibility of sub-species of *Melandrium dioicum* to attack by Aphidae.' Naturalist, No. 831: 148.

The red campion (*Melandrium dioicum*) is susceptible to infestation by the aphis *Brachycaudus* (*Anuraphis*) *lychnidis*. Of examples of the two subspecies, *villosum* and *zetlandicum*, growing in the experimental garden of the University of Leeds in the spring of 1948, 49 out of 60 *villosum* plants died before flowering due to the severity of infestation by the aphis, while only one out of 103 *zetlandicum* became seriously infested and died. This difference in susceptibility is attributed to the density of hairs on leaves and stems of *zetlandicum*, which provided a serious impediment between the aphis and the epidermis.

Blezard, E. (1946). 'The Lakeland Pennines and their birds.' Trans. Carlisle Nat. Hist. Soc. 7: 100–15.

A general survey of the birds of the fells of eastern Cumberland and Westmorland, with much information on nest-sites, food and habitat.

Collyer, E. (1949). 'The predator aspect of the fruit tree red spider problem.' Rep. E. Malling Res. Sta. 1948: 108–10.

Notes on the bugs *Blepharidopterus angulatus*, *Anthocoris nemorum* and *Orius majusculus*, the beetles *Stethorus punctillum* and *Oligota flavicornis* and the lacewing *Conwentzia psociformis*. Gives list of over 40 predators of this 'red spider' (mite) found in Essex.

Comfort, A. (1946). 'Woodland colony of *H. aspersa* in Sussex.' J. Conch. 22: 218–20.

Description of woodland habitat of *Helix aspersa*.

Cramp, S. (1949). 'The birds of Kensington Gardens and Regent's Park.' London Bird Rep. 13: 37–45.

The parks were visited weekly between October 1946 and September 1949, during which period 19 breeding and 8 non-breeding species were observed in Regent's Park and 25 breeding and 9 non-breeding species in Kensington Gardens. 17 of the 19 breeding species common to both are garden birds; the differences in the fauna appear to be due mainly to the more timbered character of Kensington Gardens and to human interference, which prevented ground species breeding in Regent's Park. The breeding population in the parks is controlled by adaptability of the species to the presence of humans, food supply (reduced by trampling and soot contamination, but increased by supplies brought by human visitors), and the scarcity of nesting sites, which must be inaccessible—the last being probably a limiting factor. Breeding densities were 9–12 birds per 10 acres in Kensington Gardens and 6–9 in Regent's Park; the density of birds feeding in the parks and winter populations are much greater. Although breeding populations vary somewhat from year to year, the number of breeding species appears to have increased, especially in Kensington Gardens, over the past 50 years.

Dicker, G. H. L. (1948). 'A preliminary report on the strawberry eelworm (*Aphelenchoides fragariae* Ritzema Bos).' Rep. E. Malling Res. Sta. 1947: 144–7.

Includes notes on habits.

Edney, E. B. (1949). 'Evaporation of water from woodlice.' Nature, Lond., 164: 321–2.

There appears to be no efficient check to the evaporation of water such as that provided by the waxy layer in insects. However, there are specific differences in resistance to desiccation.

Fitter, R. S. R. (1949). 'A check-list of the mammals, reptiles and Amphibia of the London area, 1900–1949.' Lond. Nat. for 1948, 28: 98–115.

An annotated list, giving localities, dates and indications of abundance and habitat for some 45 mammals, 8 reptiles and 8 amphibians recorded within 20 miles of St Paul's Cathedral. Of these, 32 mammals, 4 reptiles and 5 amphibians are at present feral residents, and the status of four mammals and one amphibian is uncertain. Some mammals that are expected to extend their range and enter the area are also included.

Gimingham, C. T. & Hille Ris Lambers, D. (1949). 'A new British species of *Aphis* L., from *Rhamnus catharticus* (Homoptera, Aphididae).' Proc. R. Ent. Soc. Lond. B, 18: 116–18.

Aphis mammulata found in dense clusters on the petioles of the berries with a few scattered individuals on the undersides on the leaves. Non-migratory.

Graham, R. (1946). 'The badger in Cumberland.' Trans. Carlisle Nat. Hist. Soc. 7: 88–99.

Includes general information on habitat and food.

H[arrison], J. W. H. (1946). 'Black larvae of the merveille du jour moth (*Griposia aprilina*) in Urpeth woods.' Vasculum (Substitute), 31: 30.

'Protective' black coloration found where oaks were not smoke-blackened.

Hopwood, A. T. (1947). 'British snails abroad.' J. Conch. 22: 236–42.

Discussion of effect of climatic gradients on distribution of land snails.

Jacob, F. H. (1949). 'A study of *Aphis sambuci* L. (Hemiptera: Aphididae) and a discussion of its bearing upon the study of the "black aphids". Part I.' Proc. R. Ent. Soc. Lond. A, 24: 90–8.

An account of the morphology, biology, history and synonymy of a member of the *Aphis fabae* complex found on the roots of *Silene augustifolia*.

Johnson, D. S. & Lowy, J. (1948). 'Observations on the distribution of *Helicella caperata* and *Trichia striolata*.' J. Conch. 23: 9–13.

Field observations and experiments on the preference of snails for broad or narrow leaved plants.

Le Gros, A. E. (1949). 'Notes on the spiders of the bombed sites.' Lond. Nat. for 1948, 28: 37–9.

Of 21 spiders collected during 1947–48, most were ground and hunting species or species commonly associated with buildings. Only one orb-web spinner (Argyropid) was observed, and the scarcity of this group can probably be attributed to their dislike of soot contamination, since dipterous food was plentiful. A female of the grassland species, *Euophrys aequipes*, found in leaf debris in a churchyard may have been introduced with hay. Of the two common house-spiders, *Tegenaria atrica* was abundant among rubble in the open, whereas *T. domestica* was restricted to an occasional cellar and the shells of buildings. Two females of *Oonops pulcher* on the web of a species of *Ciniflo* were probably scavengers.

Lewty, R. A. Carr- (1946). 'Aviation and ornithology in Lakeland.' Trans. Carlisle Nat. Hist. Soc. 7: 1–28.

Discusses various aspects of the relations between birds and aircraft, such as the association between certain species and airfields, the technique of observing birds from the air, bird flight movements in relation to weather conditions and to topography and tides, and the mapping of migration routes.

Mackenzie, J. M. D. (1946). 'Larch defoliation by *Orgyia antiqua*.' Scot. For. J. 60: 86–8.

On the author returning to an area of larch heavily infested with the larvae of the vapourer moth, after an absence of three weeks, almost the entire population of larvae was found to have died and decomposed into a dark treacly substance, stated to be similar to the effect on laboratory cultures of caterpillars due to bacillary septicaemia.

Massee, A. M. (1948). 'Notes on the insect fauna of sprayed and unsprayed apple orchards.' Rep. E. Malling Res. Sta. 1947: 132–4.

Forty-five species recorded on unsprayed trees.

Massee, A. M. (1948). 'Notes on some interesting insects observed in 1947.' Rep. E. Malling Res. Sta. 1947: 135–40.

Twenty insect pests and mites: the cold February and March apparently did not affect insects which overwinter in the egg stage; those hibernating as adults were affected: green woodpecker reported eating fruit bark-beetle (*Scolytus rugulosus*).

Pitcher, R. S. (1948). 'Observations on the raspberry cane midge (*Thomasiniana theobaldi* Barnes) and its association with cane blight.' Rep. E. Malling Res. Sta. 1947: 141–3.

Midge and fungus both require a wound in order to become established; natural splitting occurs in May and July, and August; as the result of larval midge feeding on the developing cork cells in patches cork production is inhibited locally; only after larval feeding does the cork tissue in the split become susceptible to fungal attack.

Salisbury, A. E. (1946). 'A copse in the Cotswolds.' J. Conch. 22: 194–6.

Account of a habitat of the snail, *Ena montana*.

Stevens, M. R. A. (1948). 'A geographical survey of the sheep-rearing industry of Knighton and neighbourhood.' Trans. Radnorshire Soc. 18: 38–45.

A discussion of the types of sheep—Clun Forest, Kerry and Welsh Mountain—kept in the area and their ecology. Two maps.

Stratton, L. W. (1946). 'Some New Forest snails.' J. Conch. 22: 197–9.

Habitats of land and freshwater Mollusca in the area of Burley.

Stratton, L. W. (1947). 'Mollusca of Wicken Fen.' J. Conch. 22: 247.

Draining of surrounding fens has resulted in the invasion of Wicken Fen by land snails not previously found there.

Thurgood, W. (1949). 'The Mollusca of the Leeds Naturalists' Club and Scientific Association's area.' J. Conch. 23: 73–83.

The distribution of Mollusca in the neighbourhood of Leeds in relation to the calcium carbonate content of the soil and water.

Walton, J. (1949). 'Woodpeckers and marble galls.' Vasculum (Substitute), 34: 7.

Woodpeckers' attacks reduced considerably the numbers of oak galls produced by *Cynips kollari* in Lambton Park.

Way, M. J., Hopkins, B. & Smith, P. M. (1949). 'Photoperiodism and diapause in insects.' Nature, Lond., 164: 615.

By increasing the length of artificial daylight during the larval period of the tomato moth *Diataraxis oleracea* it was possible to reduce the proportion of pupae in winter diapause.

Wilson, G. F. (1950). 'The broad mite.' J. Roy. Hort. Soc. 75: 69–74.

Hemitarsonemus latus, a world-wide pest with a wide range of host plants, has attacked glasshouse plants at Wisley. A brief outline of its history in Britain is given, with some details of life history, method of spread and control.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Armstrong, E. A. (1949). 'Bird life.' 152 pp., 1 colour photograph, 24 half-tones, many black and white illustrations by E. A. R. Ennion. Lindsay Drummond Ltd., London. Price 12*s*. 6*d*.

A general account of bird biology, including reference to most of the research work that has been done during the present century. The emphasis is on adaptation and behaviour, and it should serve as a valuable introduction to modern field work on birds. Actual citations are not given and there is no index.

Cumber, R. A. (1949). 'Larval specific characters and instars of English Bombidae.' Proc. R. Ent. Soc. Lond. A, 24: 14–19.

Describes the characters of the fourth larval instar of seven species of *Bombus* and *Psithyrus rupestris*.

Das, S. M. (1949). 'British Folliculinidae (Ciliata, Heterotricha).' J. Mar. Biol. Assoc. 28: 381–93.

Goodey, T. (1949). 'Laboratory methods for work with plant and soil nematodes.' Minist. Agric. Fish., Tech. Bull. No. 2: 1–19. H.M. Stationery Office, London. Price 9*d*.

Methods of collecting, killing, preparing and culturing.

Hickin, N. E. (1949). 'Larvae of the British Trichoptera: 27.' Proc. R. Ent. Soc. Lond. A, 24: 56–9.

Halesus digitatus Schranck (Limnophilidae), illustrated.

Hosking, E. & Newberry, C. (1949). 'Birds in action.' 128 pp., 70 half-tone and 8 colour photographs. Collins, St James's Place, London. Price 16*s*.

The main part of the book is the collection of photographs taken by the new high-speed flash equipment, and the text, apart from an introduction explaining the nature and application of the new technique, is confined to notes about each plate. The flight pictures of small passerines give valuable information on the positions and shapes assumed by the wing in different species and circumstances; others, including a fine series of barn owl with prey, give objective records of the food brought to the young. The introduction gives a circuit of the apparatus as used by the authors, though would-be users are left to work out their own photo-cell mechanism by which the subject takes its own photograph when it is in the zone of focus.

Macan, T. T. & Cooper, R. D. (1949). 'A key to the British fresh- and brackish-water gastropods with notes on their ecology.' Sci. Publ. Freshw. Biol. Ass., No. 13: 1–45.

A useful and finely illustrated key.

Morgan, M. J. (1949). 'Notes on the morphology of some species of Tanypodinae (Diptera: Chironomidae).' Proc. R. Ent. Soc. Lond. A, 24: 39–45.

Illustrated descriptions of larvae and pupae of eight species belonging to the genera *Anatopynia*, *Tanypus*, *Procladius* and *Pentaneura*.

Morison, G. D. (1949). 'Thysanoptera of the London Area. Part III. Key to British genera and species of Thysanoptera (contd.).' Lond. Nat. for 1948, Suppl. pp. 77–131.

Keys are given to the genera and species of the S.O. Tubulifera, with descriptions of species and genera and notes on food, seasonal appearance on plants, and distribution in Britain and London. There is also a systematic list of the British Thysanoptera, indicating type species and species recorded from the London area, and a bibliography.

Niblett, M. (1948). 'More alternating generations in Cynipidae (Hym.).' Proc. R. Ent. Soc. Lond. B, 17: 142–4.

Evidence of the connexion between the sexual and agamic generations of several species of *Andricus* and *Cynips*.

Quick, H. E. (1947). '*Arion ater* (L.) and *A. rufus* (L.) in Britain and their specific differences.' J. Conch. 22: 249–61.

The slug hitherto known as *Arion ater* really includes two species, distinguished principally by genitalia.

Stroyan, H. L. G. (1949). 'The occurrence and dimorphism in Britain of *Metopeurum fuscoviride* nom.n. (*Pharalis tanaceti* Auctt. nec. L.) (Hemiptera, Aphididae).' Proc. R. Ent. Soc. Lond. A, 24: 79–82.

Includes distribution in Britain.

3. PARASITES

Comfort, A. (1949). 'A commensal of *Lymnaea*.' Proc. Malacol. Soc. Lond. 27: 246.

The oligochaete worm, *Chaetogaster limnaei*, found commensal with the molluscs, *Lymnaea stagnalis* and *L. peregra*, at Waltham Cross, Herts. In the laboratory it infested *Planorbis planorbis*.

Cumber, R. A. (1949). 'The biology of humble-bees, with special reference to the production of the worker caste.' Trans. R. Ent. Soc. Lond. 100: 1–45.

Includes notes on parasites; the nematode *Sphaerularia bombi*, the tachinid *Brachycoma devia*, conopids and parasitic humblebee *Psithyrus*: also seasonal population changes.

Thompson, J. L. Cloudesley- (1949). 'The enemies of myriapods.' Naturalist, No. 831: 137–39.

An account of the parasites (Sporozoa, Nematoda, Acari and Diptera) and predators (Chilopoda, Acari, Araneae, Hymenoptera and vertebrates) of myriapods, in which it is concluded that enemies do not play such an important part in controlling myriapod populations as the physical conditions of the environment.

4. FOOD AND FOOD HABITS

Cook, P. M. (1949). 'A ciliary feeding mechanism in *Viviparus viviparus* (L.).' Proc. Malacol. Soc. Lond. 27: 265–71.

An account of ciliary feeding in a freshwater prosobranch mollusc.

Hartley, P. H. T. (1947–48). 'Economic ornithology—does it exist?' Bird Notes, 23: 57–60.

A stimulating critique of current assumptions in economic ornithology, demonstrating that at present there is insufficient information on the food of any British bird to prove whether or no it is beneficial or harmful to the farmer.

Lloyd, L. C. (1949). 'The larder of the red-backed shrike.' Trans. Caradoc Fld Cl. 12: 59–63.

Discusses the conditions affecting the formation of a larder; its contents, and the bird's method of stocking it.

Massee, A. M. (1949). 'Notes on some interesting insects observed in 1948.' Rep. E. Malling Res. Sta. 1948: 102–7.

Twenty-one insects: including *Apion* spp. feeding on apple foliage, cockchafer larvae roots of hops; weevils attacking strawberry roots and earwigs feeding on fruits of peach.

Peters, B. G. (1949). 'The potato root eelworm problem.' Agriculture, 55: 493–8.

Host plants of the potato root eelworm (*Heterodera roschiensis*) are potato, tomato and a few solanaceous weeds including bittersweet (*Solanum dulcamara*) and deadly nightshade (*Atropa belladonna*).

5. POPULATION STUDIES

Campbell, B. (1929). 'Pied flycatchers and nestboxes.' Bird Notes, 23: 224–30.

A preliminary account of some experiments with nest-boxes in the Forest of Dean. The proportion of boxes occupied by pied flycatchers (*Muscicapa hypoleuca*) increased from 17 to 40 per cent between 1942 and 1948. It is considered that the provision of nest-boxes has been a favourable local factor coinciding with a general eastward spread of the pied flycatcher in Britain.

Campbell, J. W. (1949). 'The breeding of the heron in the Outer Hebrides.' Scot. Nat. 61: 73–100.

An account of the remarkable increase of the breeding population of *Ardea cinerea* in this area from 1902, when the first breeding record occurred. It is suggested that depopulation of the east coast of the Uists led to a substantial decrease in human disturbance by 1920, and so made large areas of suitable nesting habitat available close to an abundant food supply which had always supported a large non-breeding population.

Elder, H. F. D. (1949). 'The appearance and disappearance of the house-sparrow as a breeding species on the Isle of May.' Scot. Nat. 61: 101–3.

An account of the unexplained fluctuations of *Passer domesticus* on this island, where it is now extinct after a fairly constant population of six breeding pairs had been maintained from 1927 to 1946.

Fisher, J. (1948). 'Natural history of the kite.' Ann. Rep. R. Soc. Prot. Birds for 1947: 22–34.

An account of the decline of the kite (*Milvus milvus*) population of Britain from abundance in the sixteenth century to an average of only three pairs in 1900–7, with a slight subsequent recovery to six pairs in 1946–47. Discusses in detail the deleterious biotic effect of man on this species, and deals also with an attempt to reintroduce it in 1927–28. Draws attention to the importance of the supply of carrion from dead sheep in maintaining the food supply of the species in its present restricted habitat in Wales.

Gough, H. C. (1949). 'Studies on wheat bulb fly, *Leptohylemyia coarctata* Fall. III. A survey of infestation in Yorkshire.' Bull. Ent. Res. 40: 267–77.

Quantitative survey in 1945; distribution discussed in relation to general observations and records in 1935-46. Only large area where it was virtually absent was on the Yorkshire Wolds.

Homes, R. C. (1949). 'Winter duck population of the London area.' Lond. Bird. Rep. 13: 46–56.

The results of counts of each of ten species on the more important waters in the London area made monthly from November 1946 till March 1948 and subsequently on six occasions until January 1949 are given and discussed with reference to weather and other factors, migration, and the results of similar regular counts in the winter of 1938–39.

Lloyd, L. C. (1949). 'Changes in the bird population of Shropshire during the present century.' Trans. Caradoc. Fld Cl. 12: 55–8.

Eight species quoted as showing a marked decrease, fourteen as showing a smaller decrease, seven as showing a marked increase and fifteen as showing a smaller increase; seven species have changed in habits. Avifauna at least as large as formerly but less varied.

Lloyd, L. C. (1949). 'Shrewsbury rookeries re-surveyed.' Trans. Caradoc Fld Cl. 12: 71.

Shrewsbury one of very few areas where rook population decreased between 1939 and 1944. Decrease estimated at 29 per cent.

Mackenzie, J. M. D. (1949). 'Tits in conifers.' Scot. Forestry J. 3 (3): 14–19.

An account of an experiment over three years with nest-boxes in coniferous woodland in Perthshire. The proportion of nest-boxes occupied rose from 9·4 per cent to 24·6 per cent, as the number of nest-boxes trebled over three years. In 1948 the order of frequency was great tit (*Parus major*), coal-tit (*P. ater*), blue tit (*P. caeruleus*), and the 'optimum potential occupation rate' is said to be much the same as in the broad-leaved woods of the Forest of Dean, Gloucestershire.

Parker, A. H. (1949). 'Observations on the seasonal and daily incidence of certain biting midges (*Culicoides* Latreille—Diptera, Ceratopogonidae) in Scotland.' Trans. R. Ent. Soc. Lond. 100: 179–90.

The peak period of *Culicoides impunctatus* and *C. pallidicornis* was July, of *C. heliophilus* late June. *C. pulicaris* and the *C. obsoletus* group showed no well-defined peaks. The sex ratio, except that of *C. pallidicornis*, was always unequal. The evening peak of *C. pallidicornis* ♀, *C. impunctatus* ♀, *C. obsoletus* group ♀ and *C. pulicaris* ♂ was around sunset; that of *C. pallidicornis* ♂ and *C. heliophilus* ♀ several hours earlier. The numbers caught were affected by wind, but not by temperature or humidity. *C. impunctatus* females were more strongly attracted to man than were females of other species.

Parrinder, E. R. (1949). 'The census of great crested grebes 1948.' London Bird Rep. 13: 35–6.

381 great crested grebes (*Podiceps cristatus*) were counted on the waters in the London area in 1948, when numbers, which in 1947 had declined by 18 per cent from the peak of 1946, had again increased and exceeded the 1946 population by 8 per cent. Non-breeding birds seemed to comprise an important proportion of the increase, which appears to be greater in this area than elsewhere in the country.

Phipps, J. (1949). 'The structure and maturation of the ovaries in British Acrididae (Orthoptera).' Trans. R. Ent. Soc. Lond. 100: 233–47.

Includes notes on seasonal development, effect of parasitism and relation between weight and maturity. It is suggested that average weight of a population may be used in estimating the maturity of a population.

Storrow, B. (1949). 'Concerning salmon caught in the fishery district of the River Tyne.' Rep. Dove Mar. Lab. (3) 10: 7–54.

The catch in 1927 was slightly better than the good catches of 1892 and 1883 and was exceeded only by that of 1882 and 1878. In 1920 and 1938 the fishery was a failure. Few fish are caught in February and throughout the following months the catches increase to a maximum in July which is followed by decrease in August. The value and seasonal sequence of categories (defined by length of life as shown by scales) and of their apparent yearly sequence are discussed; also weights and categories, year classes, the war years, fluctuations and possible correlations (e.g. sea temperatures and salinity).

Vevers, H. G. (1949). 'The biology of *Asterias rubens* L.: growth and reproduction.' J. Mar. Biol. Ass. U.K. 28: 165–187.

A study of growth and reproduction in a number of populations of the common starfish in the Plymouth area.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Anton, J. F. (1949). 'Stalked barnacles on the shores of the British Isles.' Scot. Nat. 61: 65–67.

Two instances of *Lepas anatifera* reaching British seas on a log and a raft respectively, a tropical species which only arrives attached to objects which have been at sea for a long time.

Blezard, E. & Johnston, T. L. (1943). 'The rearing of ducks at Netherby.' Trans. Carlisle Nat. Hist. Soc. 6: 17–19.

Describes extensive duck-rearing activities near the Solway Firth between 1890 and 1926, as a result of which the wigeon (*Anas penelope*), the pintail (*Anas acuta*), the gadwall (*Anas strepera*) and for a time also the mandarin duck (*Aix galericulata*) became established as breeding species in Cumberland, where they had not previously been known to nest.

Blair, K. G. (1949). (**Review.**) 'The Boreo-British Coleoptera. A study of the faunistical connections between the British Isles and Scandinavia.' By Dr Carl H. Lindroth (Motala, Sweden), 1935, in *Zoogeographica*, Band **2**, pp. 579–634. Jena.' Scot. Nat. 61: 104–11.

Draws attention to an important paper written in English in 1935 on the zoogeographical relations of the 15 species of beetle found both in Britain and in the extreme north of Europe.

Conder, P. J. (1949). 'Observations on a migration of *Pieris brassicae* L. at Skokholm Island, Pembrokeshire, in August, 1947.' Proc. R. Ent. Soc. Lond. A, 24: 35-8.

Other butterflies observed were *Vanessa atalanta*, *Pyrameis cardui* and *Colias croceus*.

Currie, P. W. E. (1949). 'Black redstarts in the London Area 1948.' Lond. Bird Rep. 13: 33–4.

The breeding records of eight pairs of *Phoenicurus ochrurus* that bred in the City and one pair that bred at Westminster are summarized, and a list given of non-breeding records from Inner London, Surrey and Middlesex. Most of the breeding males were in first summer plumage and scarcely distinguishable from females, and the importance of exercising care in recording a breeding pair on the evidence of song and the sight of an apparent female only is pointed out.

Gimingham, C. T. & Thomas, I. (1949). 'Colorado beetle in England, 1948.' Agriculture, 56: 65–70.

Finds of single beetles and 11 breeding colonies (Kent, Surrey, Berkshire, Buckinghamshire, Sussex and Worcestershire) compared with 57 in 1947. Black nightshade (*Solanum nigrum*) is a wild host plant.

H[arrison], J. W. H. (1942). 'Immigrant Lepidoptera in Durham and Northumberland in 1941.' Vasculum (Substitute), 27: 5.

Immigrants included clouded yellow, painted lady, red admiral and Camberwell beauty butterflies and silver-Y and death's head moths.

H[arrison], J. W. H. (1942). 'Immigrant Lepidoptera in 1942.' Vasculum (Substitute), 27: 30.

Only small numbers of most of the usual immigrants were seen in Northumberland and Durham.

Harrison, J. W. H. (1943). 'Immigrant Lepidoptera in 1943.' Vasculum (Substitute), 28: 30.

With the exception of the large white butterfly (*Pieris brassicae*) immigrants in Northumberland and Durham were not numerous.

H[arrison], J. W. H. (1945). 'Observations on Durham butterflies.' Vasculum (Substitute), 30: 54.

Recolonization of lost territory by small heath (*Coenonympha pamphilus*) and meadow brown (*Maniola jurtina*).

H[arrison], J. W. H. (1946). 'The progress of the elephant hawk moth in our counties.' Vasculum (Substitute), 31: 29.

Recolonization has continued and *Deilephila elpinor* has been reported from widely separated areas in Northumberland and Durham.

H[arrison], J. W. H. (1948). 'Introduced plants and insects in the Scottish Western Isles.' Vasculum (Substitute), 33: 30.

A brief note on some escapes in Lewis, Rhum, Eigg and Harris.

Rees, C. B. & Cattley, J. G. (1949). '*Processa aequimana* Paulson in the North Sea.' Nature, Lond., 164: 367.

Larvae of this decapod crustacean, previously known only in the Red Sea, Suez Canal and at Naples, are now being actively produced in the North Sea. The species may have been brought over by ships in water ballast.

Richards, O. W. (1949). 'The significance of the number of wing-hooks in bees and wasps.' Proc. R. Ent. Soc. Lond. A, 24: 75–8.

Some evidence that the number of hamuli is related to the normal flight-range of bees.

Uvarov, B. P. (1949). 'The migratory locust in England in 1947 and 1948.' Proc. R. Ent. Soc. Lond. A, 24: 20–25.

The immigration of the French race and Black Sea race with map and note on supposed immigration of *Stomorrhina lunata*, a Muscid parasite of locust eggs.

Williams, C. B. (1949). 'Migration in Lepidoptera and the problem of orientation.' Proc. R. Ent. Soc. Lond. C, 13: 70–84.

A survey of the behaviour of some typical species and a discussion of the problems connected with migration, particularly that of orientation.

7. REPORTS OF ORGANIZATIONS

Blathwayt, F. L. (1947). 'Report on Dorset birds, 1946. (With some notes up to May, 1947.)' Proc. Dorset Nat. Hist. and Arch. Soc. for 1946, 68: 93–8.

There are notes on the effect of the cold weather at the end of the year and in early 1947. The rest of the report consists of notes on 93 recorded species.

Blathwayt, F. L. (1948). 'Report on Dorset Birds, 1947.' Proc. Dorset Nat. Hist. and Arch. Soc. for 1947, 69: 125–30.

The report gives notes on 84 species and in many cases refers to the effects of the cold weather early in the year. An attempt was made to take a census of buzzards.

Blathwayt, F. L. (1949). 'Report on Dorset Birds 1948.' Proc. Dorset Nat. Hist. and Arch. Soc. for 1948, 70: 127–33.

An annotated list of 68 birds are given. The first authenticated record of the breeding of the whinchat (*Saxicola rubetra*) in the county is mentioned and the abundance of nightingales (*Luscinia megarhyncha*). December gales brought six Leach's fork-tailed petrels (*Oceanodroma leucorrhoa*) to the coast.

Farne Islands Committee of the National Trust (1946). 'The Farne Islands, Ornithological Report for 1946.' (By T. R. Goddard.) 8 pp.

The first ornithological report to be issued on the Farne Islands. Embodies the author's experiences during 16 days on the islands and includes information from watchers, etc. The effect of the war years is discussed and particularly the diminution in nesting eider ducks.

Farne Islands Committee of the National Trust (1947). 'The Farne Islands, Ornithological Report for 1947.' (By T. R. Goddard.) 8 pp.

The status of the breeding birds is dealt with; eider ducks have increased. Visitors included a hoopoe—the first recorded for sixty years.

Farne Islands Committee of the National Trust (1948). 'The Farne Islands, Ornithological Report for 1948.' (By T. R. Goddard.) 7 pp.

This is a short report, but both breeding birds and visitors are dealt with.

Freshwater Biological Association of the British Empire (1949). Seventeenth Annual Report for the year ending 31st March, 1949. 55 pp. (Price to non-members, 1*s.* 6*d.* F.B.A., Wray Castle, Ambleside, Westmorland.)

Includes an account of current research.

Lack, D. (1949). 'The position of the Edward Grey Institute, Oxford.' Bird Notes, 23: 231–36.

An account of the history of the Edward Grey Institute of Field Ornithology, now a part of the Department of Zoological Field Studies in the University of Oxford, and of its aims and current work.

Lang, W. D. (1947). 'Report on Dorset Natural History for 1946 (except birds and Lepidoptera).' Proc. Dorset Nat. Hist. and Arch. Soc. for 1946, 68: 87–92.

The second reported occurrence of the serotine bat (*Eptesicus serotinus*) in the county is recorded. There are notes on Orthoptera and records, mainly from Bryanston School, of Odonata. There are brief notes on Hymenoptera and Coleoptera and a list by Dr C. D Day of rare species of tachinid flies taken in Dorset. The local spread of the spider *Argiope bruennichi* in the south-west of the county is recorded and of the slipper-limpet (*Crepidula fornicata*) in Weymouth Bay. There is a brief note on plants.

Lang, W. D. (1948). 'Report on Dorset Natural History for 1947 (except birds and Lepidoptera).' Proc. Dorset Nat. Hist. and Arch. Soc. for 1947, 69: 120–2.

There are brief notes on the increase of the grey squirrel (*Sciurus carolinensis*) and the decrease of the red squirrel (*Sciurus vulgaris*) in three localities. Short notes follow on Orthoptera, Odonata, Diptera and a Polychaete worm.

Lang, W. D. (1949). 'Report on Dorset Natural History for 1948 (except birds and Lepidoptera).' Proc. Dorset Nat. Hist. and Arch. Soc. for 1948, 70: 121–3.

Short notes on the spread of the grey squirrel (*Sciurus carolinensis*) and the decrease of the red squirrel (*Sciurus vulgaris*) are given. Brief notes follow on Hymenoptera, Diptera and Mollusca. There is information on the spread of the slipper-limpet (*Crepidula fornicata*). A scarcity of *Cepaea hortensis* is recorded after 8–9 years abundance.

Lloyd, L. C. (1949). 'Recorder's report on vertebrate zoology.' Trans. Caradoc Fld Cl. 12: 28–38.

Almost entirely birds and mammals. Grey squirrel spreading but red still common; dormouse practically gone. First Shropshire breeding record of blackheaded gulls, on Longmynt 1942.

London Natural History Society (1949). 'Birds in the London area 1948. A report on bird life within twenty miles of St. Paul's Cathedral.' London Bird Rep. 13: 5–32.

An annotated list, giving dates, localities, numbers and other particulars of some 138 birds observed during 1948.

London Natural History Society (1949). 'City bombed sites survey.' Lond. Nat. for 1948, 28: 37–44.

In addition to a progress report indicating the scope of the work at Cripplegate during 1948 and a paper on plant ecology, this report includes notes on the spiders of the area by A. E. Le Gros [see section 1 (*c*)].

London Natural History Society (1949). 'The Survey of Bookham Common. Seventh Year.' Lond. Nat. for 1948, 28: 45–63.

In an introductory progress report of work in 1948, C. J. F. Bensley indicates the general effects on the freshwater Mollusca of refilling a pond, previously almost dry for 15 months, and clearing the streams and ditches; and P. W. E. Currie states that the observed breeding bird species, with the number of territories, found in an area of about 90 acres over which the cover was considerably reduced following the firing of the grass were chaffinch (37), reed bunting (4), yellow bunting (10), tree pipit (14), willow warbler (25), grasshopper warbler (3) and whitethroat (34). The rest of the report comprises three botanical papers and one on Coleoptera by A. M. Easton (pp. 59–63) that contains an annotated list of the hydrophilids, scarabaeids and lucanids found on the Common (representing not quite half, all and rather more than a third, respectively, of the totals for the British Isles). Particulars of seasonal appearance, habitats and abundance are given.

Russell, A. G. B. (1947). 'Report on Dorset Lepidoptera, 1946.' Proc. Dorset Nat. Hist. and Arch. Society for 1946, 68: 99–102.

The year was a poor one but there was a prevalence of melanic and melanistic moths, possibly due to delayed emergence from the pupae cause by the cold weather. 'Unbelievable' numbers of *Plusia gamma* are reported from Swanage on June 8th. An annotated list of 78 Lepidoptera is given.

Russell, A. G. B. (1948). '1947, "Annus Mirabilis" for butterflies and moths.' Proc. Dorset Nat. Hist. and Arch. Soc. for 1947, 69: 112–19.

An account is given of an 'unparalleled' year for moths and of incredible numbers of clouded yellows (*Colias croceus* (=*edusa*)). Some species new to Dorset are mentioned and several rare moths, including the first British records of *Plusia limbirena*. British resident species, however, probably due to the torrential rains of the previous autumn, were poorly represented.

Russell, A. G. B. (1948). 'Report on Dorset Lepidoptera, 1947.' Proc. Dorset Nat. Hist. and Arch. Soc. for 1947, 69: 131–4.

Lists 90 species with annotations.

Russell, A. G. B. (1949). 'Report on Dorset Lepidoptera, 1948.' Proc. Dorset Nat. Hist. and Arch. Soc. for 1948, 70: 143–6.

The year is considered to have been a poor one and there were few migrants. Notes are given on 56 species.

Royal Society for the Protection of Birds (1949). Ann. Rep. for 1948. pp. 36.

Includes a brief account of the more interesting species of birds which bred at the Society's sanctuaries at Minsmere Level (Suffolk), Grassholm (Pembrokeshire), Dungeness (Kent) and Llanddwyn Island (Anglesey), and notes on the breeding population in the British Isles during 1948 of certain rare species, including the avocet (*Recurvirostra avosetta*), the bearded tit (*Panurus biarmicus*), the golden eagle (*Aquila chrysaëtus*) and the Dartford warbler (*Sylvia undata*).

Williamson, K. (1949). 'Fair Isle Bird Observatory: First report, 1948: part I, detailed notes on species.' Scot. Nat. 61: 19–31.

Notes on voice, behaviour, migration, field characters, food and feeding habits, parasites, roosting, taxonomy and weight for twenty-nine resident and migratory bird species.